H I L G A R D I A

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 28 AUGUST, 1959 No. 19

FLIGHT ACTIVITY OF *COLIAS PHILODICE EURYTHEME* BOISDUVAL IN RESPONSE TO ITS PHYSICAL ENVIRONMENT[1]

THOMAS F. LEIGH[2] and RAY F. SMITH[3]

INTRODUCTION

NUMEROUS FIELD OBSERVATIONS of the alfalfa butterfly, *Colias philodice eurytheme* Boisduval, in the spring and summer months have indicated that flight activity of this insect is closely correlated with changes in its physical environment. In the early morning, butterflies are observed to rest, on plants, with wings folded and bodies oriented perpendicular to the sun's rays. During cool weather, flight activity stops when sunlight is temporarily cut off by clouds, and starts again when sunlight is no longer interrupted. During periods of high temperature, butterflies collect at water holes and on pond scum.

During 1952 and 1953, this insect's physical environment was investigated, to determine some of the factors that modify flight activity. Most of the study was carried out in the San Joaquin Valley of California, during the spring, summer, and fall months. Some laboratory studies were made under controlled conditions, as an aid to interpretation of the field data.

Earlier ecological investigations of *C. ph. eurytheme* have been conducted on dispersal (Smith *et al.*, 1949);[4] flight activity of color phases (Hovanitz, 1948); biology of a parasite (Allen, 1958; Allen and Smith, 1958); disease organisms (Steinhaus, 1951; Thompson and Steinhaus, 1950); and development of the reproductive system and oviposition as influenced by environmental conditions (Stern, 1952). Details of the habits of this insect will be found in these papers. Numerous observations of its activity are also recorded in the literature, but seldom include measurements of the concurrent physical factors of the environment.

Available manpower and instruments determined the limit of the investigation, which was confined to a study of total radiant energy, light, air temperature, and some moisture relationships. These by no means represent the entire physical environment, but they appeared to be most significant

[1] Received for publication March 6, 1958.

[2] Assistant Entomologist in the Experiment Station, University of California, Davis.

[3] Associate Professor of Entomology and Associate Entomologist in the Experiment Station, Berkeley.

[4] See "Literature Cited" for citations referred to in the text by author and date.

in modifying the flight activity of *Colias*. Because the physical factors are more easily dealt with individually, they are so treated in the following discussion. Obviously, such a separation is artificial since each factor is influenced to some degree by variations in the others.

Body temperature and flight activity of the adult stage were selected as measurements of the response of *Colias* to its physical environment. They were measured throughout the day under diverse physical conditions, and then correlated with the measurements of the various physical factors.

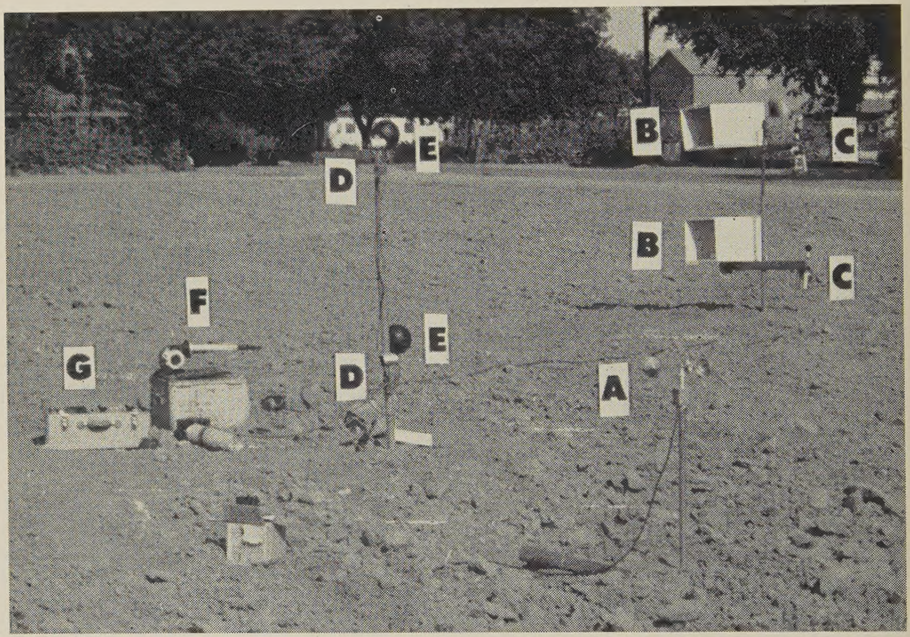

Fig. 1. Instruments used in investigation of physical environment, arranged over fallow field: *A*, anemometer; *B*, hygrothermographs; *C*, atmometers; *D*, air temperature thermocouples (within shield); *E*, globe thermometers; *F*, total hemispherical radiometer; *G*, potentiometer.

Thermocouple thermometry was used for the majority of the temperature measurements. Its application included measurement of air temperature, globe thermometers, sensitive elements of the total hemispherical radiometer, and body temperature of the adult *Colias*. Copper-constantan thermocouples were used for all locations measured (hot junctions) with a common reference (cold) junction for all. To enable the use of a common cold junction, all hot junctions of the thermocouples were joined through a dual, 12-point, silver switch housed in a small metal box. This system was similar to that of Robinson (1927). The use of a common reference junction proved very unsatisfactory since the connection provided an added source of error unless carefully checked during each series of readings.

Duplicate instruments were set up at 20 and at 60 inches above the ground (fig. 1). The lower level is considered representative of the environment in which adult *Colias* spend most of their time. The higher is representative

of the macroenvironment as measured by standard weather instrumentation. The instruments were, in part, adaptations of those developed in the Department of Agricultural Engineering at the University of California (Brooks and Kelly, 1951; Schultz and Brooks, 1956).

Some features of the population structure of *Colias* were necessarily investigated, and their relationships to the influence of the physical environment on body temperature and flight activity were recorded. Actual records for a particular period or day are presented where applicable. In other cases it was necessary to compile data for several periods or dates. Body temperature measurements, except where illustrating variations among individuals, are the means of values obtained from two to six individuals.

PHYSICAL ENVIRONMENT

Radiant energy is the most significant physical factor in the environment of *Colias* through the effects of radiant heat on body temperature and of light on behavior. (The short waves may also produce some biological effect, but this factor is beyond the scope of the present investigation.)

Sky radiation is included with solar radiation without distinction since the two could not be separated with the available instruments and since the total heat energy received was the critical value desired. According to Duggar (1936), with the sun at zenith, under normal conditions, solar radiation comprises about 92 per cent of the total, with sky radiation accounting for the remaining 8 per cent. Near sunrise and sunset the two are equal; at and after sunset, the incident radiation is entirely from the sky.

Two methods were used to investigate radiant energy relationships of the alfalfa butterfly environment: (1) measurement of the total solar and sky radiation; and (2) measurement of the black-globe temperatures. The latter used the temperature of a globe thermometer which is in equilibrium with its surroundings with respect to heat energy exchange.

Total Solar and Sky Radiation. The radiation intensity of the sun and sky was measured with a total hemispherical radiometer (also referred to as a flat-plate radiometer). This is a relatively new instrument developed at the University of California (Gier and Dunkle, 1951). It has the capacity to measure total solar and sky radiation incident upon a flat surface, regardless of ambient temperature conditions, and is nonselective with respect to wave length. Its spectral characteristics, rapid response to fluctuations in irradiation intensity, stability, and portability make it suitable for field use, but such use is restricted by the requirement of a source of electric power (110 volts, 60-cycle).

In our studies, the radiometer was mounted with the sensing element horizontal at 20 inches above the ground (fig. 2). This is near the average height of butterfly activity. The average is higher in an emergence-stage field (nearly full grown), and lower in an oviposition-stage field (recently cut). Height of this instrument is not particularly significant, but proper leveling (orientation to the sky) is. Care must be used in locating the instrument to prevent interference through reflection from or reduction of radiation by near-by buildings or other objects.

The intensity of radiation was measured at intervals of 15 to 30 minutes

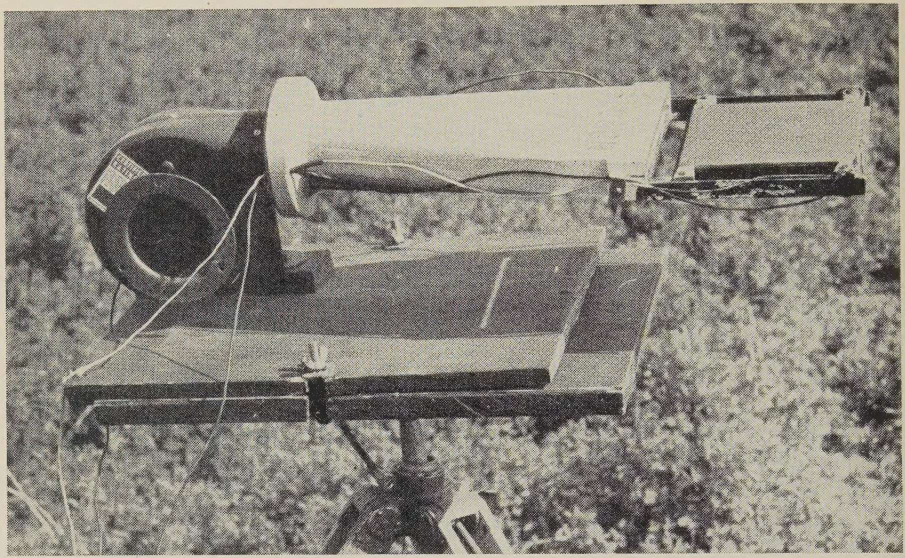

Fig. 2. Total hemispherical radiometer.

throughout the daylight hours. During periods of rapidly changing radiation intensity, such as a day with broken clouds, more frequent readings were taken. On some such days, rainfall forced discontinuation of readings.

Under usual conditions in the San Joaquin Valley the intensity of the sky radiation has been found to remain near 100 B.T.U./sq. ft./hr. during the night, with some influence by prevailing weather conditions, i.e., the moisture content of the air (Gier and Dunkle, 1951). Very shortly after sunrise on a clear day, the rate of solar radiation begins to increase rapidly, and continues to rise until the sun reaches the zenith at about noon. After midday, the radiation rate declines steadily until sunset when the nocturnal level is again reached. Observations were made from April through October. The two most common types of days were those that were clear and sunny, and those on which large, cumulus clouds obscured the sun for variable periods of time.

When the intensity of radiation is graphed against time of day, for a clear, sunny day in July, results are about as in figure 3, top. At 6:00 a.m. the intensity is already increasing and has reached about 140 B.T.U./sq. ft./hr. Peak intensity is usually reached between noon and 12:30 p.m. when the intensity is between 455 and 465 B.T.U./sq. ft./hr. Radiation intensity has usually declined to about 140 or 150 B.T.U./sq. ft./hr. by 6:00 p.m. These values are comparable with those for the Imperial Valley illustrated by Brooks and Kelly (1951), who also made comparisons with ground radiosity and net heat absorbed by the ground. The only significant influence of season on the total solar and sky radiation intensity curve is a change in its period, which is greatest during midsummer when the days are longest, and shorter in the spring and fall when the days are shorter. The length of day does not greatly influence the peak of intensity of solar

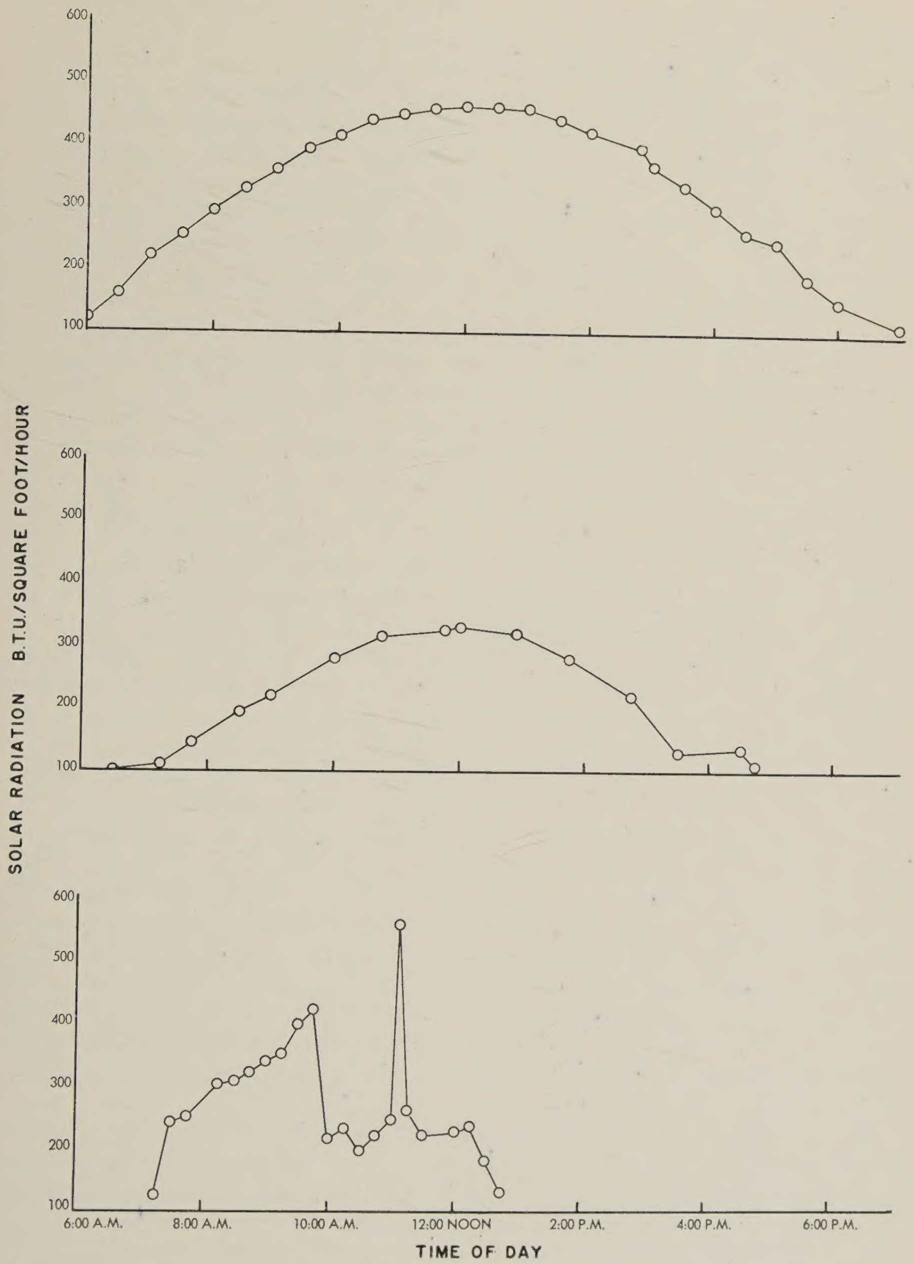

Fig. 3. Solar radiation intensity in relation to atmospheric conditions in the San Joaquin Valley on three dates. *Top:* July 25, 1953, clear, with slight smoke and dust haze (Famoso, Kern County); *center:* October 30, 1953, heavy smoke haze throughout day (Famoso); *bottom:* April 29, 1953, partial overcast with periods of direct sun and cloud reflection (11:03 a.m.), rain after 12:45 p.m. (Vernalis, Stanislaus County.)

radiation at solar zenith—the earth is closer to the sun during winter (the short-day period) although it is in the southern latitude. Kimball and Hand (1936) indicate that the maximum variation through seasonal distance from the sun is about 7 per cent. However, if the flat-plate radiometer is oriented parallel to the earth's surface, it will indicate less radiation per square foot when the sun is low on the horizon. The peak of intensity fluctuates only slightly on clear days, depending on the amount of smoke, dust, and water vapor present in the air. Each of these factors absorbs selectively from different portions of the total range of wave lengths of radiant energy (Kimball and Hand, 1936). In the San Joaquin Valley a great deal of haze is normally present during the summer months, but the peak intensity of radiation ranges around 455 to 465 B.T.U./sq. ft./hr. On occasional days the intensity may be reduced to as low as 330 B.T.U./sq. ft./hr. by heavy smoke haze, as on October 30, 1953 (fig. 3, center). When such conditions exist, the radiation is usually proportionately reduced for the entire day or for a major part of the day. On exceptionally clear days the value may be higher.

During periods of overcast weather, clouds may effect the measured intensity of solar radiation through reflection or through reduction of the radiation. When scattered cumulus clouds are present, the radiometer will frequently indicate very high radiation intensity as a result of reflection of solar radiation from the cloud surfaces in addition to the normal, direct radiation. The magnitude of the reflected radiant energy may range from so slight that it is insignificant to instances in which it exceeds the normal intensity by as much as 80 to 90 B.T.U./sq. ft./hr.

The results obtained on a day with partial overcast and rain, at 12:45 p.m. (April 29, 1953), are shown in figure 3, bottom; intensity of radiation is plotted against time of day. The very early morning was heavily overcast, with partial clearing at 7:30 a.m. The clouds again cut off direct radiation at 9:45 a.m., and were intermittent thereafter until the rain began. At 10:15 and again at 10:45 and 11:00 a.m. while direct solar radiation was still cut off by the clouds, radiation intensity increased as a result of reflection from a cloud surface. At 11:03 the cloud interruption passed, and direct radiation with cloud reflection gave a reading of 554.6 B.T.U./sq. ft./hr. Similar cloud reflections were obtained on other occasions. Coblentz (1921) and Ives (1946) have reported the effect of cloud reflection on pyrheliometer readings. Colbentz reports that clouds may reflect 78 per cent of the incident solar radiation.

When clouds pass between the sun and the position where intensity is being measured, they may cut off a large portion of the solar radiation for a period of time. The degree to which the radiation is reduced depends on the type of cloud blanket. Thin clouds may reduce the total radiation only slightly; heavy clouds may reduce it greatly. Figure 3, bottom, illustrates a reduction in intensity when large, cumulus clouds and a heavy cloud blanket prevail, in addition to the reflection mentioned above. Occasionally, a high, thin layer of clouds will reduce the intensity to a considerable degree for part or all of the day.

Black-globe Temperatures. For over 150 years, blackened bodies have been

used as indicators for intensity of radiant heat energy (Lee, 1953; Bond and Kelly, 1955). These have been of innumerable types, usually designed by an investigator to fit a particular radiant heat problem in his research. John Leslie (1804) used blackened, 4-inch spheres of tin. Vernon (1932), in his investigations of radiant heat in relation to human comfort, utilized several types of blackened spheres, including cloth, glass, and copper. He found a 6-inch copper sphere, similar to the type used as a float on a ball-cock, most convenient. When painted black (matt-black) and equipped with a thermometer, it was called a globe thermometer.

The globe thermometer is based on the principle that a blackened sphere functions as an indicator of the mean effectual radiation intensity of its environment. This globe thermometer temperature is the balance of heat gained or lost from the action of radiation, conduction, and convection. If the objects (radiant energy sources) surrounding the globe are warmer than the globe at equilibrium with the ambient air, the temperature of the globe will be raised to a point above ambient air temperature. On the other hand, when surrounding objects are cooler, the globe temperature will be below air temperature. The extent to which the globe thermometer temperature will approach the temperature of the surrounding surfaces is regulated by ambient air temperature and air currents. This difference is further complicated by the size of the blackened sphere. While investigating the use of the globe thermometer in heating and ventilation, Bedford and Warner (1934) determined that the heat loss by convection from a globe less than 4 inches in diameter may be sufficient to make results difficult to interpret, while in globe thermometers 10 inches in diameter, the time lag is too great. They found Vernon's 6-inch copper globe thermometer most satisfactory in response to convection and to lag, and superior to the other sizes where air currents are variable.

Further tests on the influence of globe size on final temperature were conducted by Kelly *et al.* (1949), and by Bond and Kelly (1955). Globe thermometers of 2 to 10 inches in diameter were tested under conditions of high radiation intensity. Results indicated that the increase in temperature with increase in diameter was rapid up to 4 to 5 inches, and was low above a diameter of 6 inches. Schultz and Brooks (1956) stated that the lags of larger globes are not a serious problem, and even suggested increasing the mass of the globes to reduce temperature unrest.

If the *mean radiant temperature* is desired, it is necessary to know the velocity of convective air movement and the true air temperature. Bedford and Warner (1934), in their investigations of heating and ventilation, developed formulas for determining mean radiant temperature and the radiant heat load from black-globe temperature, ambient air temperature, and air velocity. These are discussed in relation to agricultural problems by Bond and Kelly (1955).

The globe thermometer, as further considered in this investigation, is a hollow, blackened, copper sphere with a thermometer or thermocouple suspended at its center. Three modifications have been adapted to field studies in insect ecology at the University of California. The first utilizes a mercury-in-glass thermometer. A short tubulure is soldered around a hole

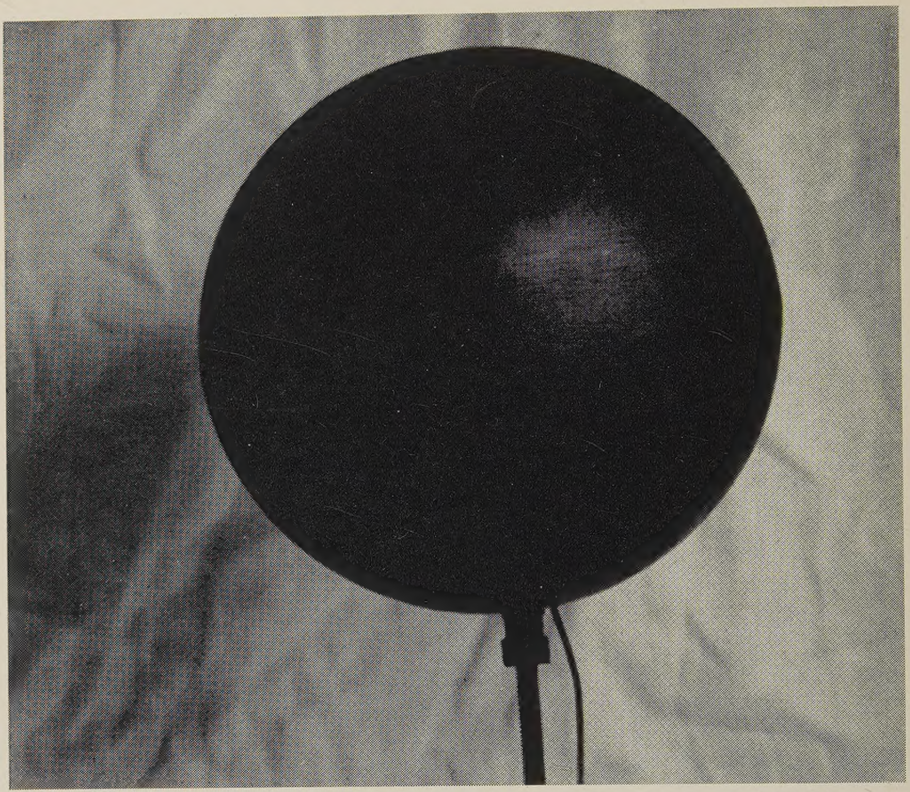

Fig. 4. Globe thermometer with copper-constantan thermocouple suspended at its center.

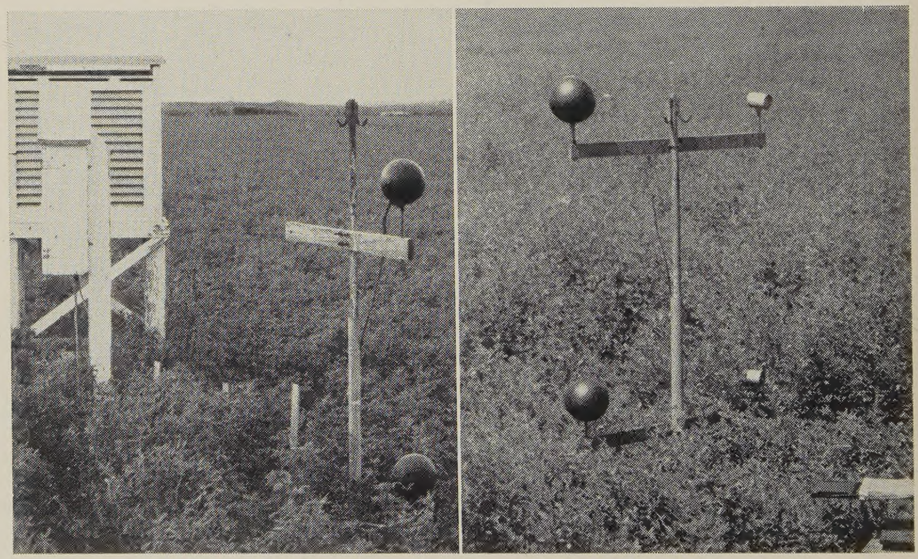

Fig. 5. Globe thermometers used to measure mean effectual radiation.

drilled in the top or side of the globe. A cork pierced by a thermometer is placed in the tubulure with the thermometer bulb at the center of the globe. In the second type, a thermocouple is suspended at the center through small holes drilled in the top and bottom of the sphere (fig. 4). The thermocouple, with thread attached, is inserted through the bottom, and the thread is run to the top hole and fastened to a pin or key. The copper spheres are painted matt-black (Kodak brushing lacquer No. 4). Care must be taken to insure that the thermosensitive element is in the center of the globe, and that the globe is handled properly, to preserve the efficiency of the matt-black finish. The third modification (fig. 5) uses the sensitive elements of a liquid-in-metal, distance-recording thermometer to obtain continuous daily records of the fluctuations of mean effectual radiation temperature in an alfalfa field, in a manner similar to the black globe in the spot-climate recorder of Schultz and Brooks (1956). Results obtained with these three modifications of the globe thermometer were similar.

In their investigations of animal shelters in hot climates, Kelly *et al.* (1949) used the black-globe temperatures directly as obtained. These workers found that, where the conditions of convective air movement and temperature are uniform for the area and height concerned, the black-globe temperatures are of excellent comparative value. In the current investigations, the greatest reliance is placed on the direct black-globe temperature readings because of the limited data on air movement. The progression of globe temperatures through the day, in alfalfa fields, is illustrated in figures 6, 7, and 8. The cycle is uniform and simple on clear summer days, as shown in figure 6 for globes at 20 and 60 inches, in an alfalfa field with 3 to 6 inches of plant growth. Shortly after sunrise, the globe thermometer rises rapidly and soon reaches levels 3 to 7 degrees C, and occasionally as much as 9 degrees above the ambient air temperature. The spread is usually greatest in the morning, and narrows as the day progresses. At night the globe thermometer drops below air temperature at the same height by 1.5 degrees or more.

This daily cycle of globe temperatures, and the temperature differences between globe thermometers at 20 and 60 inches are modified by local variations, such as alfalfa growth, irrigation, wind movement, and cloudiness.

Effect of Plant Growth. In a stubble field, the soil surface is hot, and lower hemisphere radiation is relatively high; the wind velocities at 20 and 60 inches are nearly equal; and the ambient air temperature is markedly higher at 20 inches. Under these conditions (top fig. 7) the globe temperatures at the two levels were only 1 to 2 degrees apart at sunrise and sunset. At midday the black globe at 20 inches was always markedly hotter than the globe at 60 inches; the difference ranged from 2 to 7 degrees in the fields studied.

As the alfalfa growth increases, the lower hemisphere radiation is reduced. Under these conditions (fig. 6), the globe thermometer at 20 inches will normally exceed that at 60 inches by 1 to 1.5 degrees, and on some occasions by as much as 2 degrees. At night the lower globe usually remains 3 to 5 degrees below the 60-inch globe.

In a nearly mature alfalfa field, where the stems have grown up around

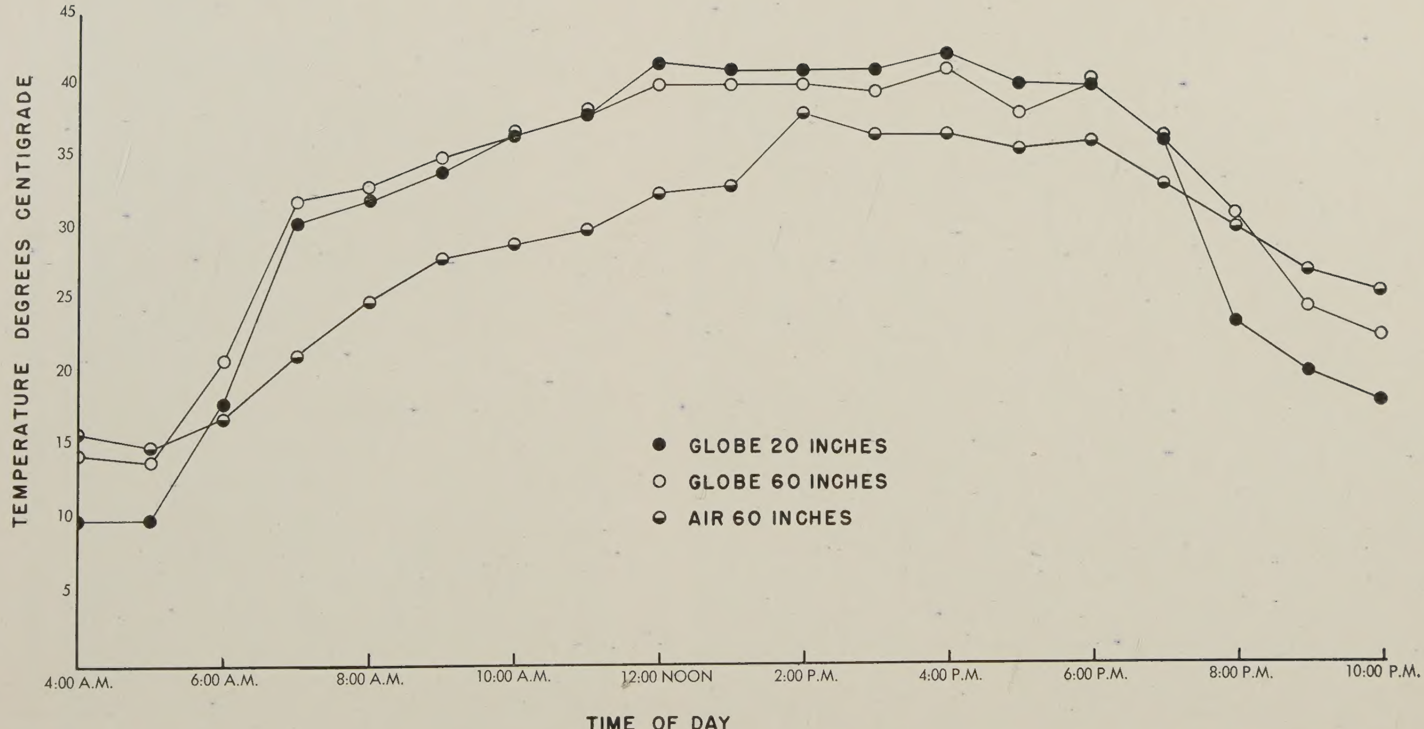

Fig. 6. Air temperature and globe thermometer temperatures over over an alfalfa field with 3 to 6 inches growth, on a clear summer day (Famoso, Kern County, July 26, 1953). (Data plotted from a Bristol recorder chart.)

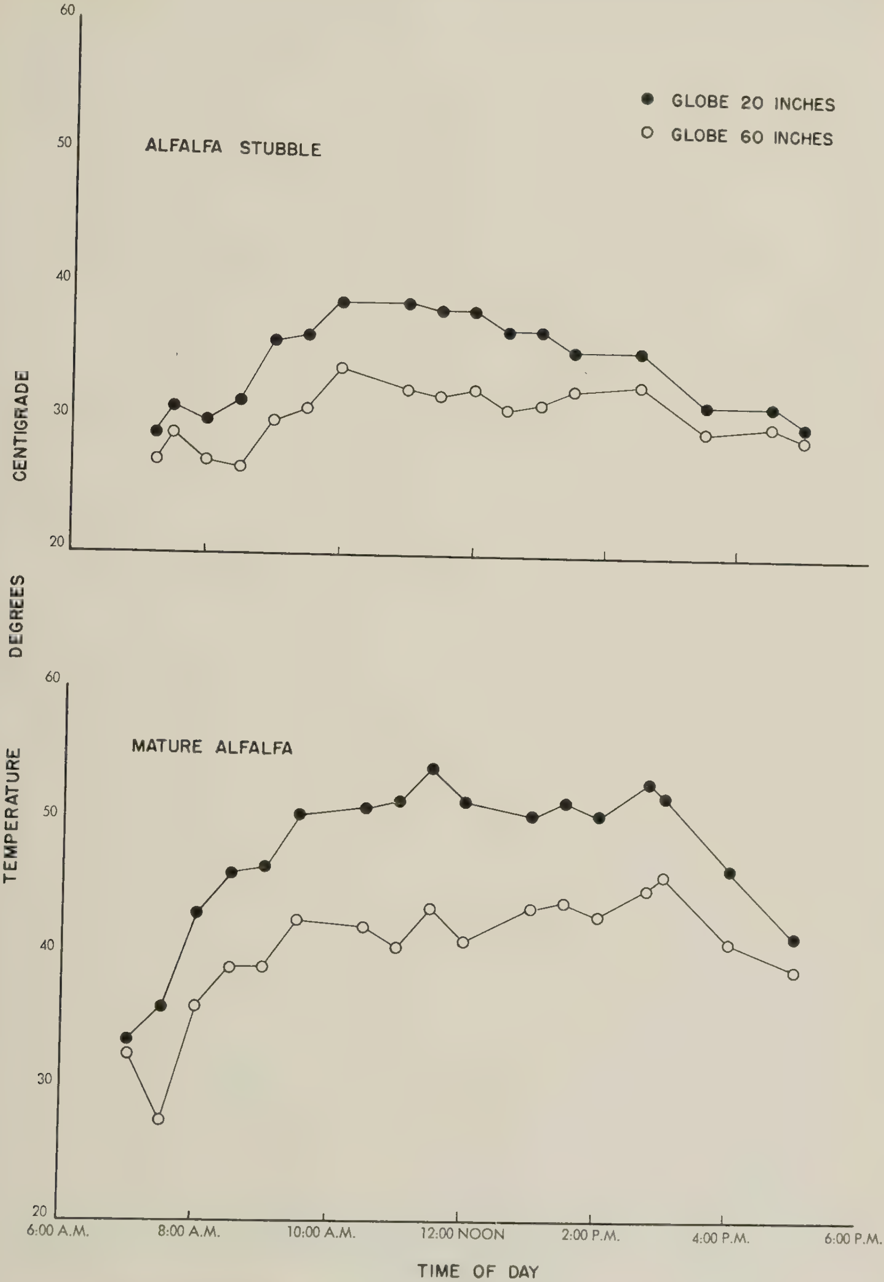

Fig. 7. Globe thermometer temperature relationships at 20- and 60-inch heights over alfalfa stubble and over a mature stand of alfalfa 18 to 24 inches tall.

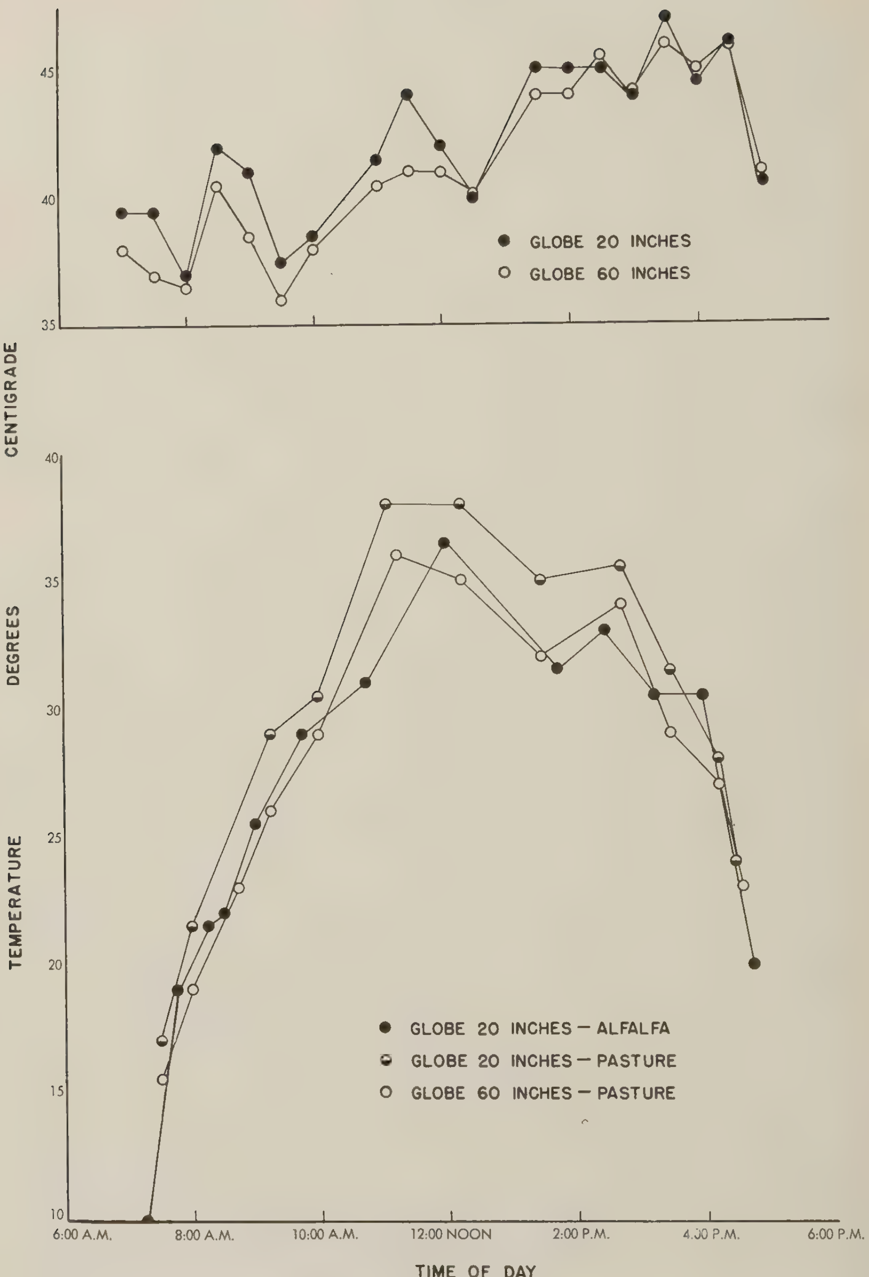

Fig. 8. Globe thermometer relationships as influenced by cultural practices and ground cover. *Top:* in an alfalfa field under irrigation (Famoso, Kern County, July 27, 1953); *bottom:* in a dry, nearly barren pasture, and in alfalfa (Famoso, October 23, 1953).

the 20-inch globe but have not covered it, lower hemisphere radiation is further reduced, convective heat loss is reduced by lowered air movement, and ambient air temperature may be modified by plant transpiration. Under such conditions (lower fig. 7), the temperature difference between the 20- and 60-inch globes is increased and, in the fields studied, the midday differential fluctuated between 5.5 and 10.5 degrees C.

When the black globe becomes covered by the alfalfa growth, shading decreases the upper-hemisphere radiation, and plant transpiration decreases the ambient air temperature. These effects may completely offset the reduced air movement, and the 20-inch globe may have a lower temperature than the 60-inch globe.

Another example of the effect of plant growth on the black-globe temperatures is shown in figure 8b, where conditions in a dry pasture are compared with those in an adjacent alfalfa field. In the pasture, the differences between the 20-inch and 60-inch globes were essentially the same as those shown for the stubble field in figure 7. The black-globe temperature at 20 inches, in the dry pasture during the midday period, was from 1.5 to 5.5 degrees higher than in the alfalfa field.

Effect of Irrigation. The radiant-heat load in alfalfa fields is often greatly reduced by irrigation. This is reflected in a reduction in difference between the globe thermometers at 20 and 60 inches in the example in figure 8, top (compare with nonirrigated field, top of fig. 7). At no time during the day does the difference exceed 2°C although the maximum at 20 inches was 47°C. This is the result of reduction in back radiation from the soil and reduction in air temperature near the soil because of the increased evaporation. This situation is more evident in a stubble or oviposition-stage field than in one where the foliage cover reduces hemisphere radiation.

Effect of Air Movement. As pointed out by Bond and Kelly (1955), the effects of wind will be greatest when the greatest difference between globe and ambient air temperature exists. The reduction in this difference that generally occurs as the radiant-heat load increases (fig. 6) is a reflection of the concurrent increasing wind velocities in the afternoon. In general the greatest differences occur in calm air in late morning. As discussed above, reduced air movement at the 20-inch level in taller alfalfa contributes to the increased globe temperatures.

Effect of Clouds. Clouds or any other objects which can cut off direct solar radiation, of course, bring about a general reduction in globe temperatures. It must be remembered that the globe thermometer has a conspicuous time constant (Bond and Kelly, 1955). Effects of clouds of very short duration (a minute or less) will not usually be noticed. However, when the solar radiation is cut off for longer periods, the temperatures will be reduced and will tend to equalize at the 20- and 60-inch levels.

Light

Light is known to exert a profound influence on the activities of numerous animals, insects included, by variations in day length, by making food and shelter evident, and by photochemical factors, to mention but a few (Allee *et al.*, 1949). In this investigation, light is considered from the standpoint

of the intensity necessary to induce and maintain flight activity of *Colias* throughout the day, provided that some other factor is not limiting.

Radiant energy, in the range between 3,900 and 7,700 Ångstrom units, is essential for the activity of *Colias* and for many other insects (Bertholf, 1931; Weiss, 1943; Andrewartha and Birch, 1954). The range of response to wave length is not known for this species, but if it is similar to that for most insects, its response will extend somewhat into the ultraviolet at one end of the scale and into the red or short red at the other end (approximately 2,537 to 7,000 Ångstrom units) (Weiss, 1943).

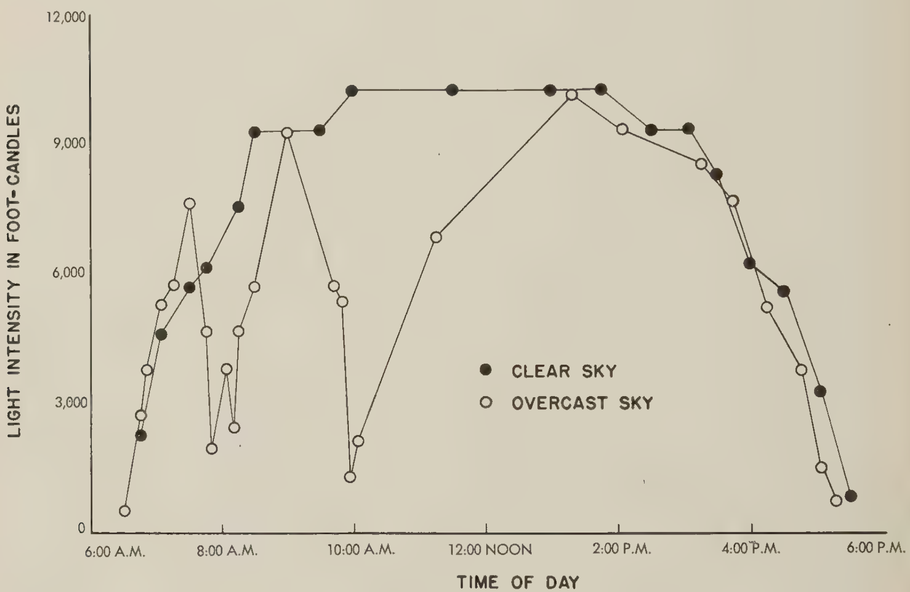

Fig. 9. Light intensity on a clear day (September 29, 1953), and on a day overcast with large, cumulus clouds through midday (October 10, 1953). (Famoso, Kern County.)

Intensity of light was measured in this study with photoelectric cells of the photographic exposure meter type. Such instruments are sensitive approximately to the same range of wave lengths visible to the human eye. This range is less appropriate for the insect eye and, furthermore, the sensitivity is not uniform across the spectrum. Nevertheless, it is a simple and satisfactory method of comparing the effects of visible radiant energy with that of the total.

In the earlier experiments a General Electric DW-48 exposure meter was used, but this was later abandoned in favor of the General Electric PR-1 meter. In measuring light intensity with the DW-48 meter, the window was directed at a piece of 8½-by-11-inch plain white bond paper held at a distance of 24 inches and so directed as to reflect the full intensity of the sun to the sensitive element. The PR-1 meter with incident light attachment was pointed directly at the sun as the intensity was read. In the following discussion both methods of measurement are considered. Since the likelihood of an error is less in the direct type of measurement, the greatest reliance is placed on the results of the PR-1 meter. With a few exceptions,

the results from the DW-48 and PR-1 meters indicate a similar daily curve when intensity is plotted against time of day.

Light intensity measurements were carried out from before sunrise until after sunset on several occasions, and usually from before the first flights of *Colias* in the morning until after the last flight in the evening. Figure 9 illustrates the curve of intensity for a typical sunny day during the summer. Light intensity increases slowly before sunrise as the "sky light" or reflection increases. In the San Joaquin Valley the intensity increases very rapidly from sunrise until midmorning (9:00 to 10:00 a.m.) when it reaches the near maximum of about 10,000 foot-candles for the day. This level is maintained throughout the middle of the day, and the decline occurs in the afternoon (2:00 to 3:00 p.m.) at much the same rate as the morning rise. The intensity may be about 150 to 200 foot-candles at sunrise and sunset. Shorter day length in the spring and fall will reduce the span of the curve but will not noticeably influence the maximum intensity. Throughout the period from September 24 to October 30, when the PR-1 meter was in use, the maximum light intensity on an average sunny day was between 9,200 and 10,200 foot-candles, with the majority of days near the lower level. For a short period on September 30, 1953, when the sky was particularly clear, an intensity of 11,300 foot-candles was registered.

Clouds, smoke, or dust, alone or in combination, may reduce the light intensity. In the San Joaquin Valley, all three of these agents may be present in varying degrees. Water vapor is not particularly absorptive of radiant energy in the visible wave lengths, but large quantities condensed into fog and clouds reduce the light intensity markedly by scattering and reflecting. Laurens (1933) found that small clouds reduce light intensity from more than 9,000 foot-candles to 3,000 foot-candles or less. In the present investigation, clouds were found to reduce light intensity from 9,200 to 1,900 foot-candles. In some instances a decline of 5,000 foot-candles occurred within a few seconds. Figure 9 shows the graph of light intensity versus time of day, for a day on which the sky was overcast with cumulus clouds during the morning, but clear in the afternoon. Laurens also found that smoke and dust, even in relatively small quantities, caused a loss of from 18 to 40 per cent of the daylight. In the present investigation, heavy smoke-haze was found to reduce the light intensity by as much as 1,500 foot-candles.

Ambient Air Temperature

The significance of air temperature in the physical environment of *Colias* is direct in its effect on the insect's temperature, and indirect in its relationship to relative humidity and to the evaporative power of the air.

Ambient air temperatures were measured with thermographs and with shielded thermocouples. Two thermographs were placed at 20 and 60 inches above the ground, in laminated, corrugated cardboard shields, open at two ends and painted white (fig. 10). The open ends were directed north-south to protect the sensing elements (Bourdon tubes) from direct solar radiation and to permit free air movement through the shield. One hygrothermograph was placed in an instrument shelter (Stevensen screen) at 60 inches above the ground.

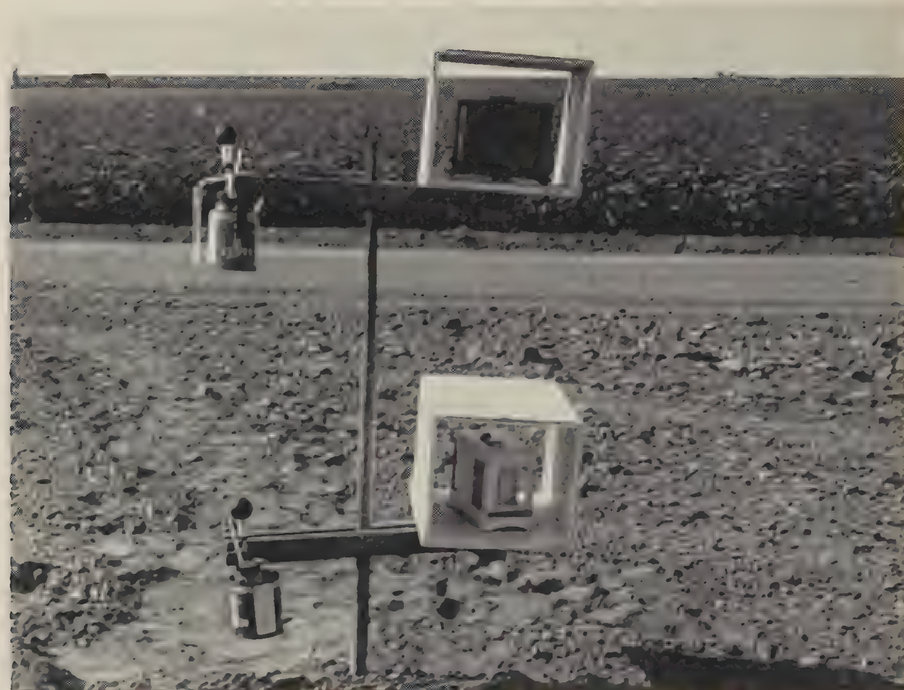

Fig. 10. Bendix-Friez hygrothermographs, model 594, as used within shield to investigate relative humidity and air temperature of the environment.

Fig. 11. Shielded copper-constantan thermocouple used to measure ambient air temperature.

Copper-constantan thermocouples were suspended by their leads in the center of a cylindrical shield, 2 inches in diameter and 3 inches long, made from a tinned can with the two ends removed (fig. 11). These shields, similar to those of Kelly *et al.* (1949), protected the thermocouples from direct solar radiation and from most of the sky radiation. The units were placed at 20 and 60 inches above the ground.

The minimum air temperature in alfalfa fields usually occurs at or shortly before sunrise. The minimum temperatures at 20 and 60 inches may be equal, but more commonly the temperature is from 0.5 to 3 degrees lower at the lower height. The temperature increases rather gradually to reach its maximum in early or mid-afternoon. At that time, it is usually from 0.5 to 3 degrees higher at 20 than at 60 inches. The afternoon decline is quite rapid near sunset. Temperature relationships such as these have been covered in detail by Geiger (1950) and others. The difference between air temperature at 20 and at 60 inches is greatly influenced by the groundcover, weather conditions, cultural practices, and other related factors which also affect globe thermometer temperatures in much the same way.

An exception to the usual relationship (higher afternoon temperature at 20 than at 60 inches) occurred in a field during irrigation. In this case, the temperature at 60 inches was equal to or exceeded that at 20 inches by as much as 1.5 degrees. This reversal can be explained by the evaporative cooling that resulted from low relative humidity on this particular day—18 per cent at 60 inches and 24 per cent at 20 inches. Figure 12, top, shows the usual conditions on a summer day; figure 12, center, shows the temperature relationship just described.

The influence of alfalfa growth on air temperature is well illustrated by figure 12, bottom, in which the temperature over an alfalfa hay field is compared with that of a dry pasture. The air temperature over the alfalfa usually remained from 0.5 degree cooler in the morning and evening to 2 to 4 degrees cooler at midday.

Moisture

Moisture, as liquid and vapor, is essential to *Colias* for development and survival. It is of indirect importance through its modifying influence on other factors of the environment, such as solar radiation.

Relative humidity of the air, as an indication of general moisture conditions, and black atmometer evaporation rates, as an indication of desiccating conditions, were studied.

Much confusion exists in entomological and ecological literature concerning the measurement of moisture and the significance to insects of relative humidity, vapor-pressure deficits, and other indications of moisture (Uvarov, 1931; Leighly, 1937; Andrewartha and Birch, 1954; Edney, 1957). As pointed out by Buxton (1930; 1932) and others, the insect must maintain its water content. It responds to a complex environment in attempts to balance water loss and water intake. This balance, in a terrestrial insect, will be governed by its habits, sources of free water, and the desiccating power of its environment. The latter is a complex of factors, most significant of which are probably body temperature of the insect, and movement, mois-

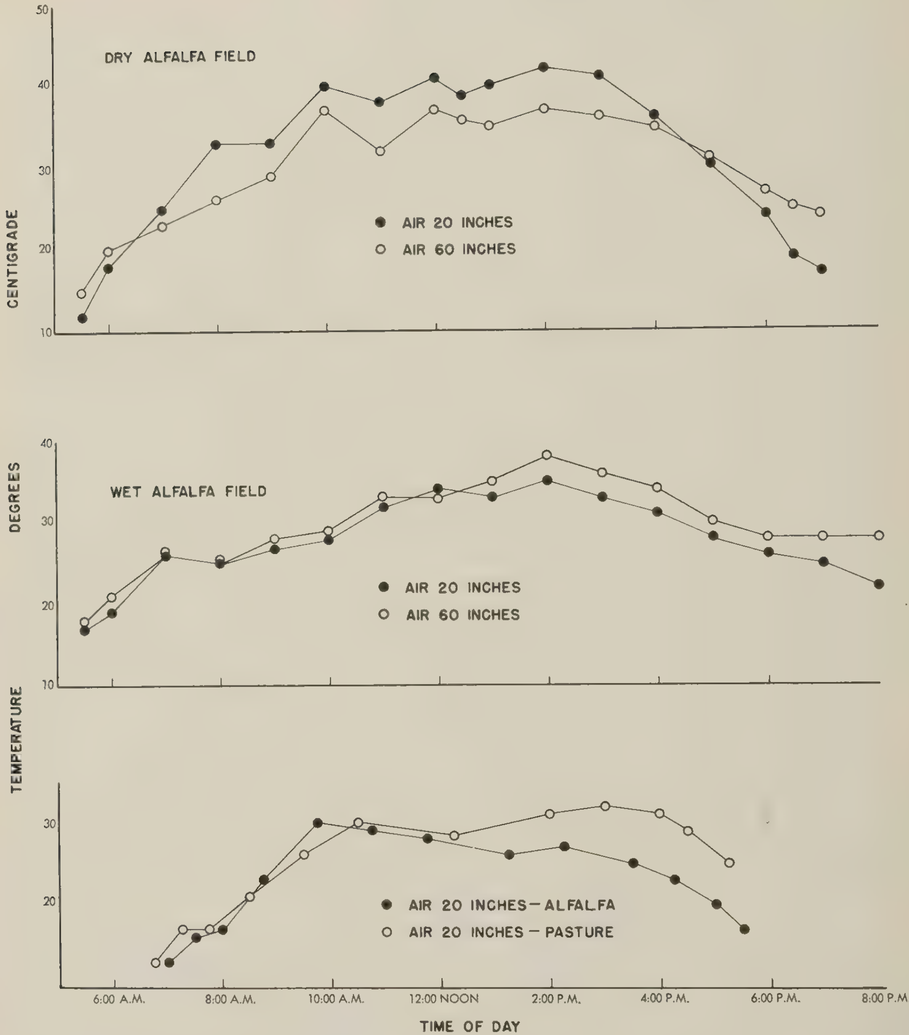

Fig. 12. Ambient air temperature in relation to cultural practices and field conditions. *Top:* relatively dry alfalfa field with 20 to 24 inches growth (July 25, 1953); *center:* alfalfa field with 6 to 8 inches growth, while under irrigation (July, 28, 1953); *bottom:* alfalfa field and a dry pasture (October 28, 1953). (Famoso, Kern County.)

ture content, and temperature of the air. It is obvious that no measurement of moisture content will be correlated with the insect's response to the desiccating power of the air unless the other factors making up this complex are constant. Because this is rarely the case in heterogeneous field environments, we feel that the evaporation rates from the black atmometer gave the most significant values.

Relative Humidity. As indicated, relative humidity alone will not give an adequate description of moisture conditions. In any analysis, it must be

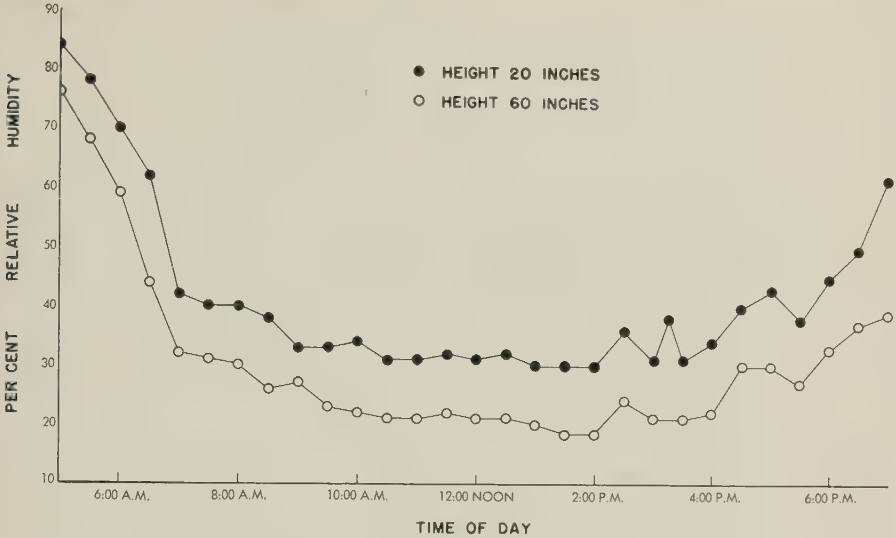

Fig. 13. Relative humidity above an alfalfa field on a typical summer day. (Data plotted from a hygrothermograph chart for July 28, 1953, at Famoso, Kern County.)

considered along with air temperature, air movement, and other factors.

Relative humidity was measured by hygrothermographs equipped with hair hygrometers (fig. 10). Accuracy of this type of instrument may be uncertain because of difficulty in keeping it calibrated during periods of dry, dusty, or rapidly fluctuating conditions, but it was the best available to us for field use. A significant advantage of this type of instrument is that a continuous and permanent record of relative humidity can be made.

The San Joaquin Valley is a region of low rainfall. For example, the normal seasonal rainfall for Fresno is 9.49 inches, with an average of only 0.28 inch from June to September. Although extensive irrigation has modified the humidity, day-time humidities are normally quite low.

Figure 13 shows a typical relative humidity record in an alfalfa field on a summer day. Soon after sunrise the relative humidity falls rapidly and then maintains a rather stable, low level until late afternoon. At night, it rarely fails to reach 80 per cent or higher at 20 inches. In the summer, the day-time minimum usually drops to below 20 per cent at 60 inches, and below 25 per cent at 20 inches. In the spring and fall, the minimums are more variable, but usually range between 30 and 35 per cent at 20 inches.

Relative humidity is strongly modified by irrigation, plant growth, and prevailing weather. During periods of irrigation, the relative humidity at 20 inches is frequently 30 per cent higher than that in nonirrigated fields. Transpiration by the alfalfa plants also increases the humidity—an effect conspicuous at the 20-inch level, but only slight at the 60-inch level.

Evaporation. The black Livingston atmometers (Livingston, 1915) were used in measuring the evaporative power of the air to introduce the influence of solar radiation as much as possible. Their construction was similar to that of Chalkley and Livingston (1929), which eliminated taking of timed

Fig. 14. Atmometric equipment used to investigate rate of water evaporation: *A*, atmometer; *B*, resistance element; *C*, manometer.

readings. Porcelain soil points served as resistance members, and quart Mason jars were used for water reservoirs. The mercury manometer was constructed of hard glass tubing of approximately 4-mm bore. This was maintained in a vertical position along the side of the jar (fig. 14). The resistance created in this unit was read as centimeters of mercury differential between the ascending and the descending columns. Since the instrument was not operated during rainy periods, the Livingston-Thone valve was not installed. Although this instrument is designed to be instantaneous, in actual practice there was a slight lag in adjustment to a sudden change in relative humidity and to wind velocity.

Christiansen *et al.* (1930) found that water temperature affects the resistance that will be created as water is drawn through the resistance member. The viscosity of the water decreases with increasing temperature; thus

the instrument reads at a lower head of mercury with increasing temperature. A mercury thermometer was maintained in the water reservoir near the resistance member. With the aid of the equations and tables of Christiansen, the readings were transposed to a standard water temperature of 20°C.

The rate of evaporation, under standard conditions, is different for each instrument, the extent of the difference being determined by the inherent characteristics of the atmometer and the resistance member. Since several atmometers were used, and the desired information was a comparison of the rates of evaporation at each location, it was necessary to determine the rates of evaporation for each unit under standard conditions and to develop a means of equating them. For this purpose a system of standardization similar to that of Christiansen *et al.* (1930) was used. In the present study, atmometers and resistance members were standardized and used as units, rather than as separate elements.

Atmometers were placed at 20 and 60 inches above the ground, in alfalfa fields in various stages of growth, and in dry pasture. Evaporation records were taken in these situations in conjunction with other physical data and observations of butterfly activity. The field arrangement of the atmometers is shown in figure 10.

Figure 15, top, shows the evaporation rate at 20 and 60 inches, on a summer day, in an alfalfa hay field with growth 6 to 8 inches tall. The evaporation curve follows quite closely that of air temperature (fig. 12), except that the peak evaporation intensity will usually fall a little later in the afternoon. The rate of evaporation is very low in the early morning, and may even have a negative value during periods of dew formation. With sunrise and evaporation of the dew, the rate of evaporation from the atmometer increases rapidly, and by midmorning may be more than 14 cc per hour. The peak rate of evaporation usually is not reached before midafternoon when, on some days, it may be more than 21 cc per hour. The decline in evaporation in the late afternoon is also very rapid, and the rate usually drops below 7 cc per hour by sunset. This implies that relative humidity is less significant than air movement since it remains near a steady state throughout most of the midday period while the rate of evaporation steadily increases. Evaporation will usually continue into the night until the wind stops and dew formation begins.

The rate of evaporation is usually the same at 60- and 20-inch heights, in the presunrise hours. After sunrise, the rate increases more rapidly at 60 than at 20 inches, until by midmorning it may be from 1.5 to 2.5 cc per hour greater. This increase may continue until, at the extreme, midafternoon evaporation at 60 inches is from 6 to 8.5 cc per hour greater than at 20 inches. The difference then gradually decreases, but may still be as great as 4.8 cc per hour at sunset. The decrease continues through the evening hours.

The difference in rate of evaporation at 60 and 20 inches is affected by the amount of plant growth, which influences vapor pressure and wind velocity. According to Geiger (1950), not only does the vapor pressure increase rapidly below 20 inches, but also wind velocity diminishes rapidly

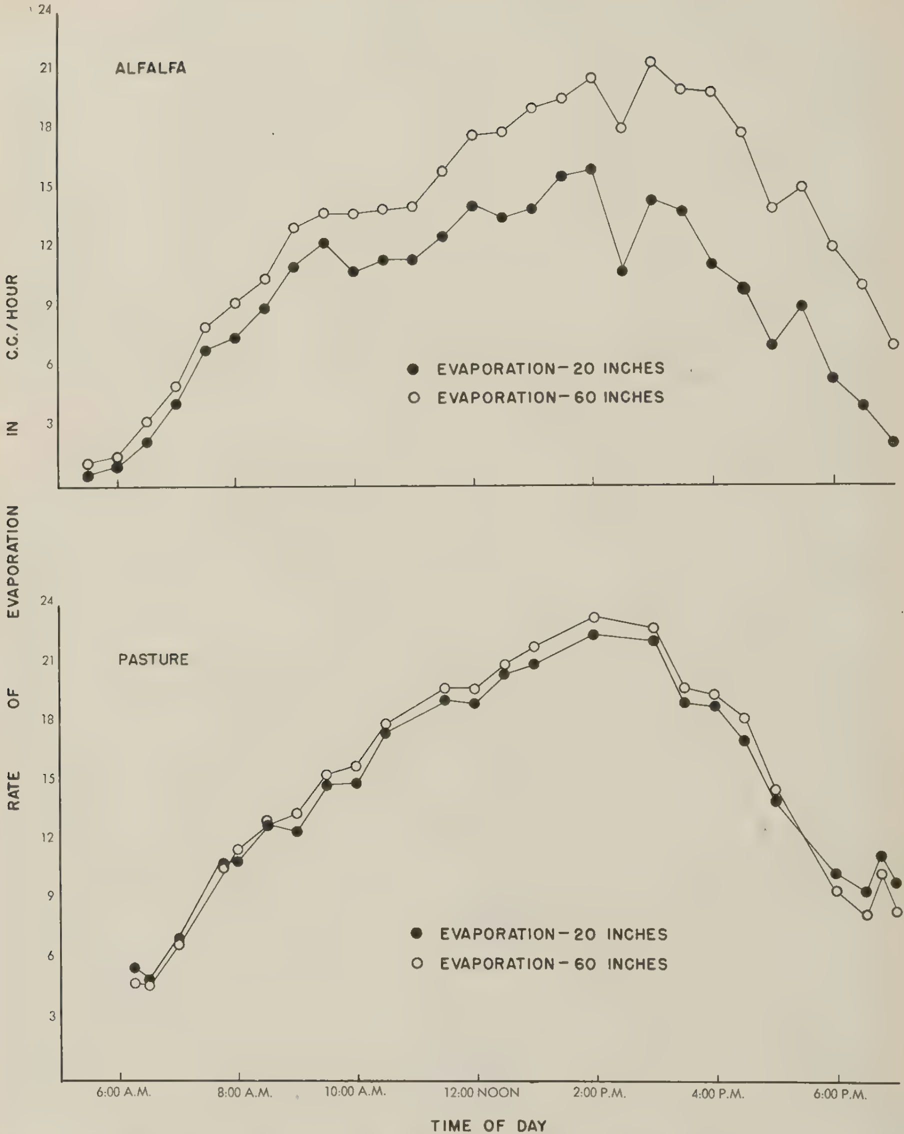

Fig. 15. Comparison of rate of water evaporation from Livingston atmometers in alfalfa (July 29, 1953) and dry pasture (July 13, 1953). (Famoso, Kern County.)

when the ground has some plant cover. Increased height of the alfalfa has the effect of lowering the 20-inch atmometers and bringing them into a region of greater moisture and less wind. This change has little or no effect on the atmometer at 60 inches (fig. 15). The temperature is usually greater at 20 inches, but the higher vapor pressure due to plant transpiration and the lower rate of air movement due to friction reduce evaporation rates.

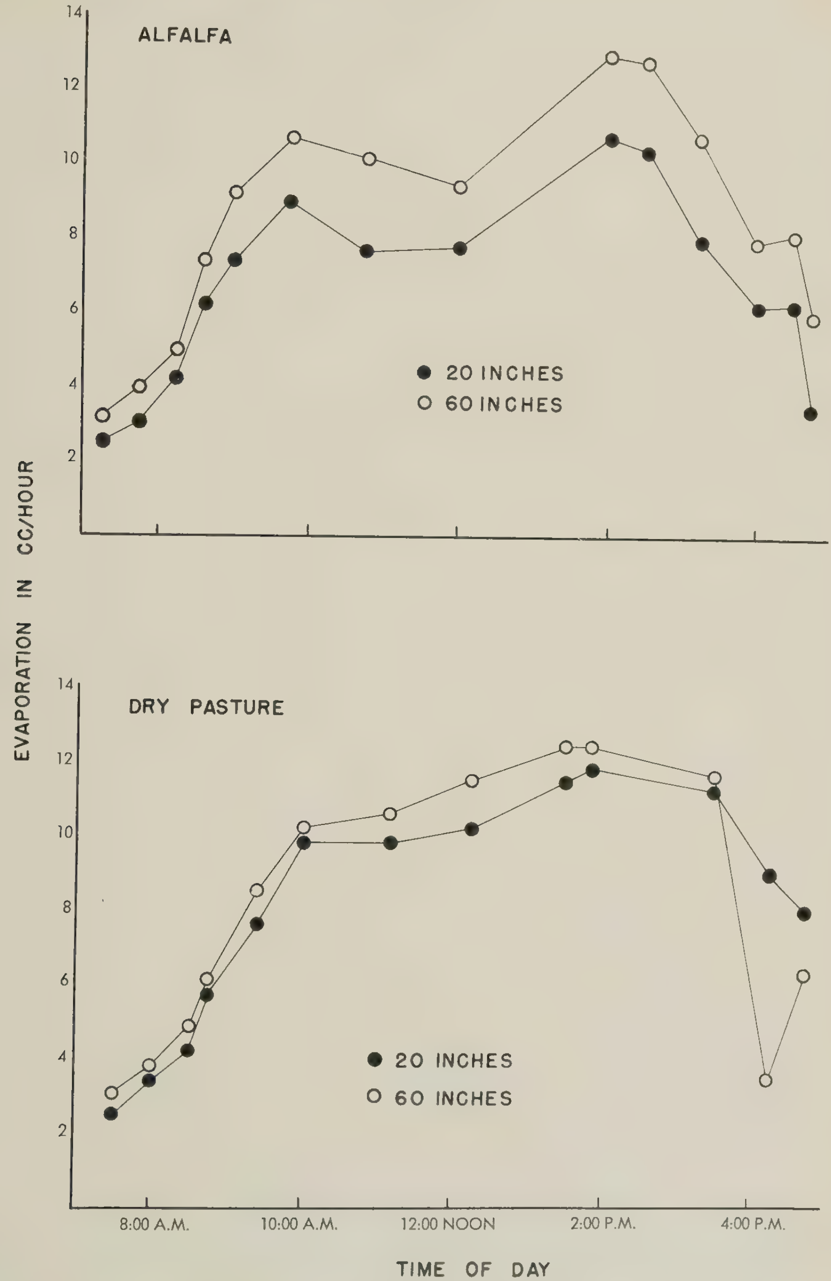

Fig. 16. Comparison of rate of water evaporation from Livingston atmometers above an alfalfa field, and at the same heights above dry pasture (Famoso, Kern County, October 23, 1953).

The difference in rate of evaporation at the two levels, over a stubble field or dry pasture (fig. 16), is reduced by an increase in the rate at 20 inches. It was less than 1.0 cc per hour at the peak period of evaporation in the example shown. Geiger indicates that, over bare ground, the vapor pressure remains the same down to about 8 inches, below which it shows a rapid increase. In addition, the wind velocity is greater at 20 inches in the absence of vegetation. It is interesting to note that, over dry pasture where the soil moisture content is very low and all vegetation is dry, the rate of evaporation at 20 inches exceeds 21 cc per hour (see fig. 15, bottom), in mid-afternoon. In alfalfa fields with similar weather conditions but with green plant cover 3 to 8 inches tall, the maximum evaporation rate (at 20 inches) seldom exceeds 18 cc per hour, and with growth 18 to 24 inches tall or more, it seldom exceeds 11 cc per hour.

A comparison of the rates of evaporation in an alfalfa field and a dry pasture in October indicated that the maximum evaporation rate at 60 inches is about the same in both field types (fig. 16). The rate of evaporation at 20 inches, in a dry pasture, approaches very closely the rate of evaporation at 60 inches, while in the alfalfa field the rate of evaporation at 20 inches will usually be lower by 3 cc per hour or more throughout most of the day.

The major variable affecting the daily course of evaporation rates in alfalfa is air movement, which follows a characteristic daily cycle. Brief interruptions in wind movement also cause rapid fluctuations in evaporation rates. Furthermore, wind movements can introduce an entirely different kind of air (wetter or drier, hotter or colder) into the alfalfa field.

RESPONSE OF *COLIAS* TO SOME ENVIRONMENTAL FACTORS

A population of *Colias* adults may be classified by sex, color, and age. The males are, with rare exceptions, yellow, and the females are either white or yellow (Remington, 1954). Earlier investigations have noted a great deal of variation in sex ratios from one field to another (Smith *et al.*, 1949) and color phase ratios from one area to another (Hovanitz, 1944; 1948). For this reason it was necessary to determine if the sexes and color phases showed any differential responses to the factors selected for study. Consequently, separate observations were made in most experiments on the activity of the males, the white females, and the yellow females. Except for the elimination of obviously injured or badly worn individuals, in the body temperature studies, no attempt was made to classify the study population according to age. This is not considered a serious omission.

Body temperature and flight activity of the adult butterflies were selected as the most suitable responses for study because relatively large samples could be drawn with ease, the responses could be observed over a wide range of physical conditions, they appeared to be consistent, and they were relatively easy to measure. It is, of course, realized that these responses are not independent, but inseparable, since flight is dependent on adequate body temperature.

Flight Patterns by Sex and Color Phase

The reasons for the relative numbers of males and females in any individual field are complex and can be considered here only in general terms. The sex ratio of *Colias* is usually accepted to be 1:1 (Gerould, 1911). The population encountered in any individual field may vary considerably from this ratio, and the composition is usually determined by the general field conditions. Female butterflies normally concentrate in recently harvested fields where the regrowth of alfalfa is not over 8 inches high. Males are more frequent in old fields of nearly mature alfalfa where the females are emerging. Counts from seven fields are given in table 1. Fields 1, 2, and 6 represent

TABLE 1
COMPARISON OF NUMBERS OF MALE AND FEMALE *COLIAS* IN FIELDS OF VARIOUS GROWTH STAGES
(Wasco, California, 1953)

Field number	Date	Field condition	No. of males	No. of females	Males
					per cent
1	July 25	Emergence stage, alfalfa 24–30 inches	1,613	443	78
2	July 26	Emergence stage, alfalfa 24–30 inches	1,889	458	80
3	July 27	Oviposition stage, alfalfa 4–10 inches	901	401	69
4	July 28	Oviposition stage, alfalfa 4–10 inches	945	318	75
5	August 30	Oviposition stage, alfalfa 3–8 inches	57	117	33
6	August 30	Emergence stage, alfalfa 24–30 inches	536	342	61
7	October 15	Oviposition stage, alfalfa 4–10 inches	186	242	43

those in which adults of both sexes are emerging, and the females are moving out to oviposition-stage fields. Fields 5 and 7 represent the oviposition-stage fields in which the female butterflies have accumulated. Fields 3 and 4 show how the usual situation was further complicated when all near-by emergence-stage fields were cut, and males were forced into the oviposition-stage field.

In order to determine the color ratio, white and yellow females were counted in 12 fields on eight dates in June, July, and August. Two methods of counting were used. In the first, the butterflies were identified by sight, according to sex and female color phase, as they flew between two stakes set 30 feet apart. This method gave greater total counts, particularly at low population levels. In the second method, the field was swept nonselectively with an insect net, and the captured butterflies were separated according to sex and color phase.

Table 2 shows the results, separated into five daily time intervals. The data were also totaled, and the unweighted per cent white for each time interval was determined from the total. The per cent white females varied greatly within each time interval as well as between intervals, with a low of 21 and a high of 75. The total numbers of some of these counts were so low that a difference of one or two individuals influenced the percentage or ratio to a very great extent; with higher counts, the variation in ratio

TABLE 2

VARIATIONS IN RATIO OF WHITE AND YELLOW FEMALE *COLIAS* THROUGHOUT DAILY FLIGHT PERIOD
(Wasco, California, 1953)

Date	Time of flight and ratio white to yellow														
	6–9 a.m.			9:01–11 a.m.			11:01 a.m.–1 p.m.			1:01–3 p.m.			3:01–7 p.m.		
	No. white	No. yellow	White	No. white	No. yellow	White	No. white	No. yellow	White	No. white	No. yellow	White	No. white	No. yellow	White
			per cent			*per cent*			*per cent*			*per cent*			*per cent*
June 14	...	...	..	27	44	38	16	21	43	12	13	48	26	36	42
July 25	14	20	41	44	38	54	48	32	60	44	41	52	94	71	57
July 26	79	87	48	71	65	52	19	34	36	23	20	53	14	19	42
July 27	71	57	55	40	26	61	3	3	50	21	7	75	97	73	57
July 28	59	46	56	45	36	56	10	7	59	2	1	66	64	48	57
August 14	263	220	54	332	304	52	128	153	46	47	60	44	310	374	45
August 14	287	274	51	238	228	51	65	91	42	42	43	49	161	174	48
August 16	210	235	47	287	329	47	168	171	50	74	78	49	333	324	57
August 16	283	261	52	163	184	47	180	200	47	161	159	50	384	425	47
August 30	8	8	50	60	93	39	62	70	46	37	51	42	65	93	41
August 30	3	2	60	3	11	21	8	6	57	10	12	45	27	35	44
August 30	7	14	33	42	42	50	32	35	48	36	29	55	46	59	44
Total and unweighted percentage	1,283	1,224	51	1,352	1,400	49	811	879	48	509	514	50	1,621	1,731	48

Fig. 17. *Colias* arranged on thermocouples for measurement of body temperature. Note $\frac{1}{16}$-inch supports used to hold thermocouple and grasped by butterfly for support. Four butterflies mounted parallel and found perpendicular (not clearly evident) to sun's rays.

was much less. These results indicate that the ratio of white to yellow female butterflies was very near 1:1 in the Wasco region of the San Joaquin Valley at the time studied, and where adequate samples were drawn there was no indication that the ratio varied through the flight day.

These results are not entirely in accord with the findings of other investigators (Hovanitz, 1948; Ford and Dowdeswell, 1948). Hovanitz reported an average white to yellow ratio near 1:1 (52.7 and 53.7 per cent white) in the Bakersfield area which is very similar to that of Wasco. However, he reported declines in white female butterflies, on three count dates, from 54, 55, and 59 per cent, respectively, to 48, 43, and 38 per cent, at midday, with a return to 50, 53, and 54 per cent in the late afternoon.

Throughout the course of this investigation, bright sunlight in the midday hours made detection of white female butterflies difficult, and particular caution was necessary to prevent overlooking these individuals in any site count method. This factor may account for the midday decline in per cent white female activity in the report by Hovanitz.

Body Temperature

Body temperature was measured with probe-type, copper-constantan thermocouples, inserted through the ventral side of the abdomen forward into the thorax. These butterflies were supported in the desired position at about 20 inches above the ground (the height at which they are usually most active) (fig. 17).

TABLE 3

COMPARISON OF BODY TEMPERATURES, BY SEX AND COLOR PHASE, OF *COLIAS* EXPOSED UNDER EQUAL CONDITIONS OF INSOLATION

Date	Body temperature (°C)			Body temp. differences between:		
	Male	Yellow female	White female	Yellow female and male	White female and male	White female and yellow fem.
				degrees	*degrees*	*degrees*
May 5	31.5	....	29.7	...	1.8	...
May 6	24.2	24.2	....	0.0	...	...
July 25	28.7	30.7	28.3	2.0	−0.4	−2.4
July 26	30.2	31.0	31.0	0.8	0.8	0.0
July 27	....	32.7	32.5	...	...	−0.2
July 27	28.2	27.2	28.5	−1.0	0.3	1.3
July 27	....	37.7	38.5	...	...	0.8
July 28	....	35.7	36.5	...	...	0.8
July 28	....	32.7	31.3	...	...	−1.4
September 24	....	29.7	30.7	...	...	1.0
September 25	....	27.0	26.7	...	...	−0.3
September 26	....	22.5	22.2	...	...	−0.3
September 29	....	30.5	30.2	...	...	−0.3
September 30	27.7	27.7	....	0.0	...	...
September 30	25.0	28.0	25.3	3.0	0.3	−2.7
October 9	25.3	26.3	26.7	1.0	1.4	0.4
October 10	19.5	20.3	19.5	0.8	0.0	0.8
October 10	23.2	....	22.5	...	−0.7	...
October 10	27.5	....	26.7	...	−0.7	...
October 10	23.2	23.2	....	0.0	...	...
October 15	20.5	21.0	20.5	0.5	0.0	−0.5
October 15	26.3	26.0	26.0	−0.3	−0.3	0.0
October 16	14.5	14.2	15.0	−0.3	0.5	0.8
October 16	....	21.5	22.0	...	...	0.5
October 16	17.5	17.5	17.5	0.0	0.0	0.0
October 17	....	19.5	20.2	...	...	0.7
October 17	....	18.3	18.5	...	...	0 2
October 20	....	24.0	24.0	...	...	0.0
October 22	....	23.0	23.3	...	...	0.3
October 23	....	25.3	25.0	...	...	−0.3
October 23	29.7	29.7	28.7	0.0	1.0	1.0

Manipulation of the butterflies caused unavoidable physical injury which, along with extreme environmental conditions and no recourse to moisture, shortened their lives. After some experience in handling the adult butterflies, abnormal individuals were not difficult to detect through one or more of the following reactions: unusual increase in body temperature over that of the other specimens; softening of the body under slight pressure from the fingers; depression of the wings; a slow response or none, to contact stimuli. Insertion of the thermocouple caused injury to the body wall and the internal thoracic tissues. Undoubtedly this disturbed the butterfly's physiology (Robinson 1928; Uvarov, 1948). However, its body temperature remained uniform for considerable periods after the insertion, and became erratic only when the butterfly appeared to be deteriorating. It is therefore assumed that the temperatures recorded were normal. The maintenance of butterflies under suitable conditions on thermocouples ranged from as little as 15 minutes

TABLE 4

COMPARISON OF BODY TEMPERATURES OF THREE YELLOW AND THREE WHITE FEMALES, AND TWO MALES OF *COLIAS* AT THREE TIMES OF DAY
(October 15, 1953)

Time of day	Body temperature (° C)							
	Yellow females			White females			Yellow males	
	1	2	3	4	5	6	7	8
8:48 a.m.	25.5	24.0	23.5	24.5	22.7	23.0	25.7	25.3
	23.5	25.5	19.7	23.5	23.0	22.7	25.3	25.3
1:40 p.m.	29.5	30.6	28.0	26.5	30.3	30.0	28.5	30.3
	29.3	30.4	28.3	26.3	29.0	29.0	28.3	29.0
	30.3	31.0	28.3	26.7	29.7	29.7	28.5	28.7
3:45 p.m.	27.5	27.3	29.7	28.0	30.4	30.7	27.3	30.3
	28.7	27.0	30.6	28.0	31.0	31.3	26.3	30.5
	26.5	27.5	27.7	27.5	28.0	28.0	26.7	27.7
	27.3	27.0	27.7	27.0	28.0	27.3	27.0	27.7
Mean	27.6	27.8	27.1	26.4	28.0	28.0	27.1	28.3

to as much as five hours, with an average of nearly two hours. The longer periods occurred early in the day and on cooler days when activity was low.

Butterflies for body temperature measurement were collected from fields in the same area where the physical and flight activity measurements were made. They were usually collected from plants in bloom along the field margin, shortly before being used. Occasionally, collections were held overnight in an ice box, for use early the following day. Selection among the butterflies available was limited to the discarding of obviously old, worn individuals.

In all body temperature experiments, from two to eight specimens (usually four) were observed simultaneously. Specimens of both sexes and yellow and white phases of the female were compared. Similar experiments were conducted with individuals oriented with wings parallel or perpendicular to solar radiation.

Relation to Sex and Color Phase. A difference in the body temperature of the sexes and color phases of *Colias* under the same or similar conditions of exposure could cause differential response to the environment. In order to determine if differences exist, male and white and yellow female butterflies were subjected to the same conditions of insolation. The results are shown in tables 3, 4, and 5. Table 3 summarizes the mean body temperature for all individuals, by sex or color, and the differences in temperature for each. Tables 4 and 5 give more detailed information for particular days, and provide a better indication of the variation encountered. The greatest difference in temperature between the sexes or the female color phases (table 3) was 3 degrees on September 30. Most differences were 1 degree or less. It is of interest to note that, for the 14 days on which com-

TABLE 5

COMPARISON OF CHANGES IN BODY TEMPERATURE, BY SEX AND COLOR PHASE, OF *COLIAS* THROUGHOUT ONE DAY

(October 15, 1953)

Time of day	Body temperature (° C)			Body temp. differences between:		
	Yellow males	White females	Yellow females	Yellow female and male	White female and male	White female and yellow fem.
6:35 a.m.	8.5	8.7	9.0	+0.5	+0.2	−0.3
6:45 a.m.	11.5	11.3	11.7	+0.2	−0.2	−0.4
7:00 a.m.	15.3	14.5	15.3	0.0	−0.8	−0.8
7:15 a.m.	17.3	16.3	16.7	−0.6	−1.0	−0.4
7:20 a.m.	17.5	16.7	17.5	0.0	−0.8	−0.8
7:35 a.m.	17.7	17.3	17.7	0.0	−0.4	−0.4
7:45 a.m.	19.0	18.5	18.7	−0.3	−0.5	−0.2
8:00 a.m.	22.7	22.5	22.0	−0.7	−0.2	+0.5
8:15 a.m.	24.0	23.5	24.3	+0.3	−0.5	−0.8
1:15 p.m.	26.5	24.5	28.0	+1.5	−2.0	−3.5
2:00 p.m.	26.7	25.7	28.0	+1.3	−1.0	−2.3
2:48 p.m.	29.5	30.2	29.0	−0.5	+0.7	+1.2
3:00 p.m.	29.0	29.7	30.0	+1.0	+0.7	−0.3
4:00 p.m.	24.7	26.5	26.0	+1.3	+1.8	+0.5
4:25 p.m.	24.0	25.0	25.0	+1.0	+1.0	0.0
4:37 p.m.	21.5	22.3	22.3	+0.8	+0.8	0.0
4:53 p.m.	19.0	19.5	19.7	+0.7	+0.5	−0.2
5:05 p.m.	16.5	17.0	16.5	0.0	+0.5	+0.5
Mean	20.8	20.5	21.0	+0.25	−0.07	−0.43

parisons could be made between females and males, the yellow females averaged 0.46 degree warmer than the males, and the white females averaged 0.29 degree warmer. The mean difference between the white and yellow females for 25 days was 0.01 degree.

Table 4 shows successive readings on six female and two male butterflies during relatively short periods on October 13, 1953. These results indicate the variation between individuals at the same time and the variation of an individual butterfly during a period of from one to three minutes. The variation in successive temperature measurements of an individual was occasionally as great as 2.5 degrees C, and between individuals of the same sex and color phase, as great as 4 degrees.

The average body temperature was recorded from two male, three white female, and three yellow female butterflies during the early morning and afternoon of one day (table 5). Variations as great as 2 degrees C exist between sexes and color phases. However, when the temperatures for the day were averaged, the differences between the means were 0.5 degree or less. When the differences were averaged, they were comparable. The yellow females tended to be warmer than the males, especially in the afternoon when the heat load was greatest.

The lack of difference in body temperature, at least between the white and yellow female color phases, is not necessarily in opposition to the results obtained by Hill and Taylor (1933), Bodenheimer (1934), and Strelnikov

(1936), with locusts. Strelnikov, working with *Locusta migratoria gregaria* (yellow-black body color) and *L. m. solitaria* (green body color), found that the darker phase had a body temperature 4.5 to 5.2 degrees C above that of the lighter phase, under equal direct exposure to solar radiation. These two color phases of *Locusta* are basically quite different in pigmentation, physiology, and receptivity to irradiation, and are not of the same body mass. The pigmentation of the wings of the two female color phases of *Colias* is quite different; however, the white phase contains appreciable amounts of yellow. The upper wing surface contains areas of black pigmentation which are different in the sexes. However, the butterfly normally folds its wings when at rest, so that only the underwing surface, which shows little black pigmentation, is exposed directly to the insolation. This habit of exposure will minimize differences in color of the two phases since the underwing surface and body of both color phases of female are similar in pigmentation except for the considerable amount of white in the white phase. It is probable that the conspicuous wings have little influence on body temperature. The results given below on the effect of the angle of incidence of radiation bear this out.

In a study similar to that of Strelnikov (1936), Pepper and Hastings (1952) found differential response rate in grasshoppers of different color, but did not find the final temperature to be different. These workers were using direct solar radiation with exclusion of incidental radiation from the ground, sky, and other objects. Much of that incidental radiation falls in the range of 3 to 50 microns—that of heat waves.

Kelly *et al.* (1949) pointed out that, although the reflectance of red, white, and black pigs is high in the short-wave energy range, the absorption in the range from 5 to 50 microns is about the same. This similar absorption of the heat wave lengths will mask an expected differential. Since much of the radiant energy of 3-micron length or greater has its origin in the ground, surrounding objects, and the sky, this may account for the difference in the results of Strelnikov and of Pepper and Hastings (1952). A temperature difference which might exist in *Colias* may be minimized through similar action.

Since Strelnikov (1936) was working with what are considered two distinct physiological races (Roeder, 1953), physiological relationships may be associated with the difference in body temperature that he obtained. His results indicate no difference in body temperature when the locusts were placed in the shade; however, this does not preclude the possibility of a differential physiological response under direct insolation. No differential activity in the two female color phases of *Colias* has been observed which would indicate differential physiology.

From the results of temperature measurements, it is evident that body temperature of the individual varies greatly under experimental exposure to direct sunlight. However, it may be concluded that, on the average, the body temperatures of the males, and of the white and yellow females are the same. All appear to be sufficiently similar to have nearly the same thermal qualities.

Relation to Physical Environment. The physical factors most significant in

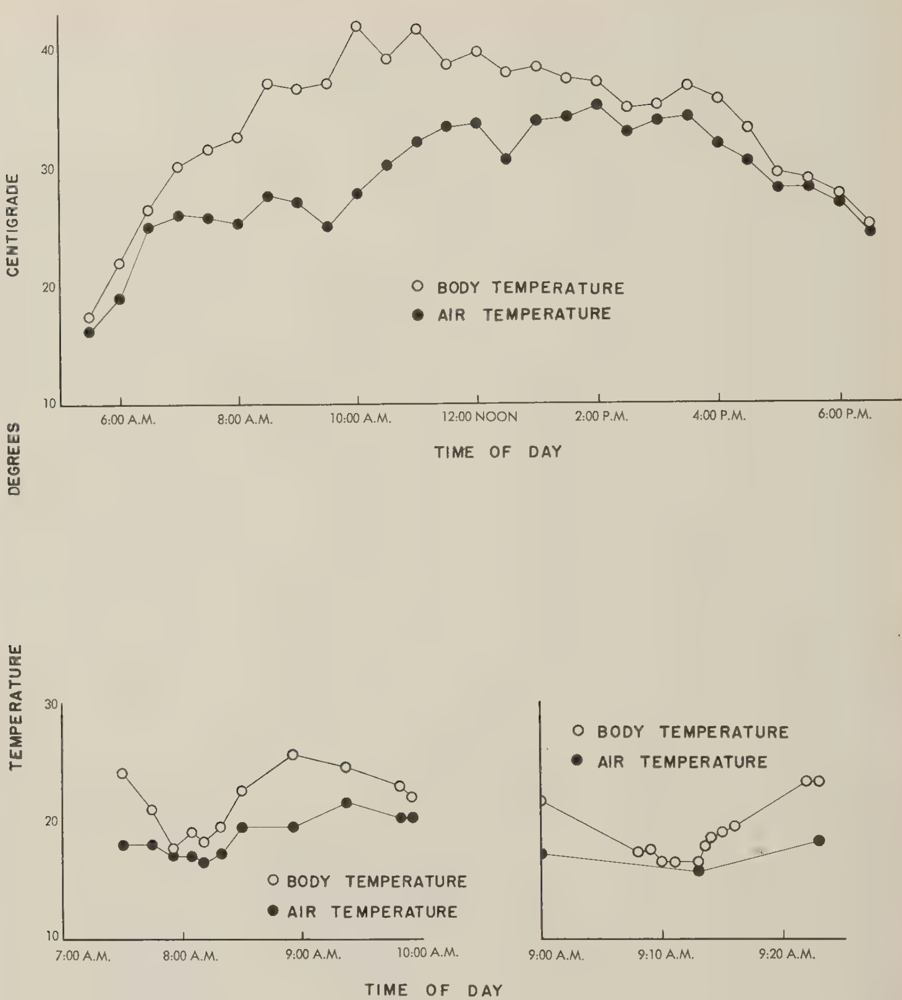

Fig. 18. Ambient air and body temperature relationships in *Colias*. *Top:* clear summer day (July 28, 1953); *lower left:* sky clear at 7:30 a.m., increased cloud at 8:00 a.m., decreasing clouds to 9:00 a.m., increasing again at 10:00 a.m. (October 10, 1953); *lower right:* interruption of direct solar radiation by a single large cloud between 9:06 and 9:20 a.m. (October 23, 1953). (Famoso, Kern County.)

the modification of body temperature of *Colias,* are ambient air temperature and solar radiation. In the absence of direct solar radiation, at night or during clouded weather, body temperature is equal to or slightly above air temperature. As solar radiation intensity increases in the morning, the body temperature of *Colias* will rise more rapidly than air temperature. This body temperature will remain higher than that of the air until radiation intensity has diminished, near sunset. During the summer months, body temperature will reach its maximum in the late morning and remain about the same until mid- to late afternoon, when it will decline to that of the air. Air

temperature increases more gradually, and reaches a peak during midafternoon. The widest difference between air and body occurs in the early morning to midday period. In figure 18, top, a typical graph of the body and air temperatures for a summer day, the peak of body temperature is near the time of peak solar radiation intensity. The decline in body temperature thereafter, in spite of increasing air temperature, may be the result of decreasing radiation intensity and of greater air movement which results in greater evaporative and convective cooling.

The curves for air and body temperature during the spring and fall are similar to those in the summer except that the peak of body temperature in the spring is more likely to occur after midday, and temperatures are generally lower. The peaks of air and body temperature may be reached at any time after midmorning as a result of local weather conditions.

The extent to which body temperature will exceed that of the air is regulated by the intensity of solar radiation, radiation from the ground and surrounding objects, moisture relationships, air movement, and body orientation. Radiation from the ground and from plants is low compared with sky and solar radiation during the daylight hours, in an alfalfa field with a good groundcover of growth. In stubble where growth is still quite short, and over dry, bare ground, radiation from the ground is considerable. Brooks and Kelly (1951), in an illustration of heat exchange over dry, bare ground in the Imperial Valley, indicate a value of 290 B.T.U./sq. ft./hr.

To understand the influence of solar radiation on body temperature, it is necessary to understand some aspects of radiation intensity and the insect's adjustment to them. Under a clouded sky, body temperature is equal to air temperature. During intermittent periods of sun and cloud, body temperature fluctuates from above to equal that of the air. The effects of both natural clouds and artificial shade on body temperature were studied. Figure 18, lower left, shows the effect of natural clouds on body temperature as compared with air temperature under a progressively changing cloud condition. There was a difference of 6.8 degrees C between air and body temperature with a clear sky; in 26 minutes, with increasing cloud cover, the difference dropped to 0.5 degree (fig. 18, lower left). When the clouds had thinned, one hour later, the difference was 6 degrees, but this lessened in one hour, as the clouds gradually thickened, to 1.5 degrees. Figure 18, lower right, represents the passing of a large cumulus cloud, during which the difference between air and body temperature dropped from 4 to 0.2 degree in 10 minutes and, in an additional 13 minutes, increased to 5 degrees.

When a piece of cardboard was used as an artificial cloud, the effect was more drastic (fig. 19, top). In this case, almost all the upper hemisphere radiation was cut off and the body temperature dropped 7 degrees C, to equal air temperature, in about three minutes. On re-exposure to solar radiation, the original temperature was again attained in about three minutes. Figure 19, lower left, is similar to 19, top, except that the comparison is between body temperatures of individuals shielded from and exposed to upper hemisphere radiation. Shielded individuals showed a drop of as much as 7 degrees C below the temperature of exposed individuals, in three minutes. On re-exposure, this loss was largely regained in three minutes.

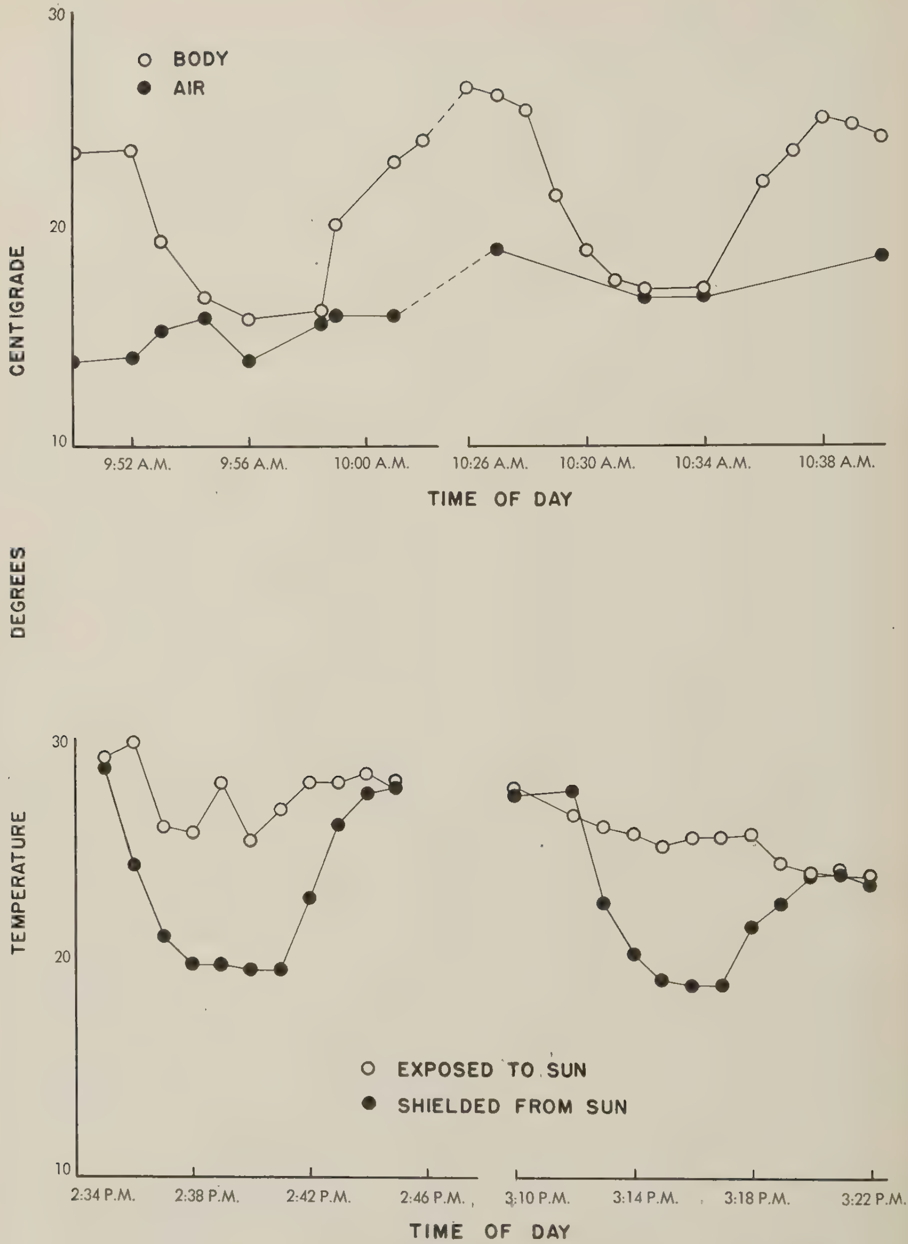

Fig. 19. Effect of artificial shading on air temperature and on the body temperature of *Colias*. *Top:* artificial shade introduced at 9:52 and 10:28 a.m., and removed at 9:58 and 10:34 a.m., respectively; *bottom:* artificial shade introduced at 2:35 and 3:12 p.m., and removed at 2:41 and 3:17 p.m., respectively. (Famoso, Kern County, October 24, 1953.)

Relation to Orientation to Solar Radiation. Adult *Colias* and other insects have been observed to cease flight when solar radiation is reduced by clouds (Guignon, 1936; Frazer, 1951), and to orient to radiation sources (Fraenkel, 1930). In the late afternoon or early evening, during the summer, the *Colias* alight either low on the plants or on the ground. They seldom remain on the ground overnight, but will remain on plants near ground level. At or shortly after sunrise, the butterflies move up the plant or other support and orient their bodies in such a way that the greatest surface, i.e., side of the thorax and abdomen, is exposed nearly perpendicular to the sun's direct rays. The insects remain in that position until body temperature is sufficiently high to make flight possible. In the spring and fall, when daytime temperatures are near the minimum level for flight, similar response may be seen at any time of day.

Butterflies have also been observed collecting on bare, dry ground and on black asphalt road surfaces in the early morning or on cool days, presumably to warm the body and makes continued flight possible.

Colias have often been observed exposing a minimum body surface to the sun during periods of extremely high air temperature and radiant heating. This orientation is very probably a response for regulating body temperature in the same or a similar manner as that determined for hymenopterous and lepidopterous larvae by Wellington *et al.* (1951), and for *Locusta migratoria* by Strelnikov (1936). These workers found the larvae to be photopositive when cool and photonegative when hot, with orientation similar to that of *Colias*.

During midday, when air temperature is very high and body temperature is likely to be greatest, *Colias* collect on moist soil and at irrigation water pools. This prevents desiccation, and may also be an effective means of lowering the body temperature by the evaporative cooling of the soil.

A number of experiments were made to determine the effect of orientation to solar radiation on body temperature. Butterflies were suspended on probe thermocouples and oriented with the side of the thorax and the wings either perpendicular to or parallel with the sun's rays. A body temperature differential became evident as soon as the orientation departed from parallel by as little as 15 degrees, and the maximum difference seemed to be realized as rapidly at an angle of 45 degrees as at an angle of 90 degrees. Here again sex and color phase did not influence the results. Strelnikov (1936), in investigations of *Locusta migratoria*, found similar body temperature responses to solar radiation. His differences were greater than those found in the case of *Colias*, a fact which may be accounted for by color and body mass factors which are markedly different in these two insect groups.

The difference in body temperature between butterflies oriented perpendicular with and parallel to the sun's rays fluctuated from zero or nearly so to as much as 5.5 degrees C difference in some cases. It usually remained between 3 and 4 degrees. These temperature differences are rapidly reduced under a clouded sky, and do not exist if the clouds are sufficiently dense. Table 6 shows data from butterflies oriented perpendicular and parallel to the sun's rays during part of a clear day. In this particular case, the least variation between individuals was less than 2 degrees C, and the great-

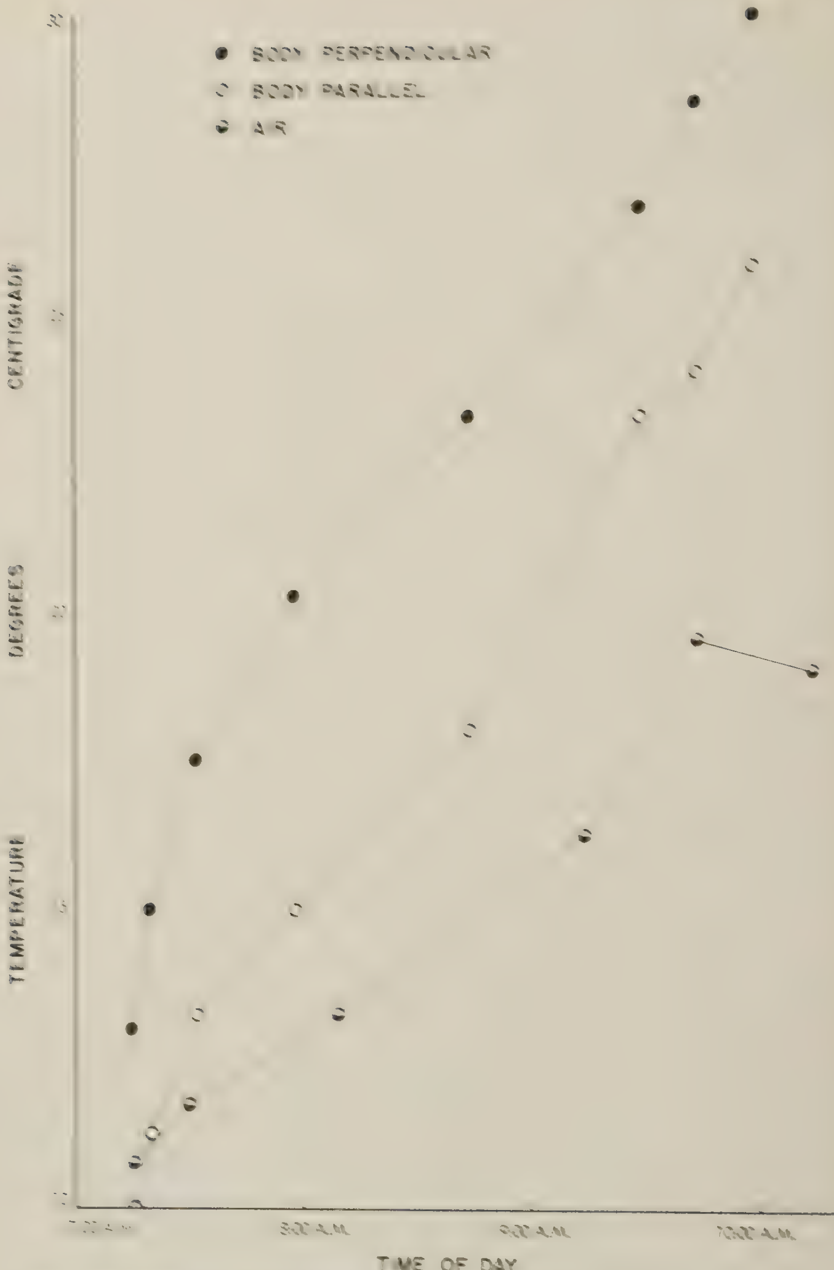

Fig. [illegible] Influence of orientation to source of solar radiation on body temperature of [illegible] as related to ambient air temperature.

[illegible]

[illegible]

[illegible] was from 1.5 degrees. In more extreme cases the temperature differences were influenced to a large degree by clouds and wind. Figure 25 represents the average temperatures [illegible] in Table 4 and indicates the relative frequency of differences between the two groups. [illegible] air temperatures [illegible] for the same period is also included.

Flight Activity

Flight activity, although indicative of flower visitation [illegible], is difficult to interpret since flight is [illegible] to many of the important physical factors of the environment as well as to the inherent behavior patterns of the insect. Any physical factor or combination of factors may [illegible] the regulation of flight at a particular time [illegible]. Flight is closely correlated with body temperature which is in turn [illegible] by several factors of the physical environment, primarily solar radiation, air temperature and air movement. [illegible]

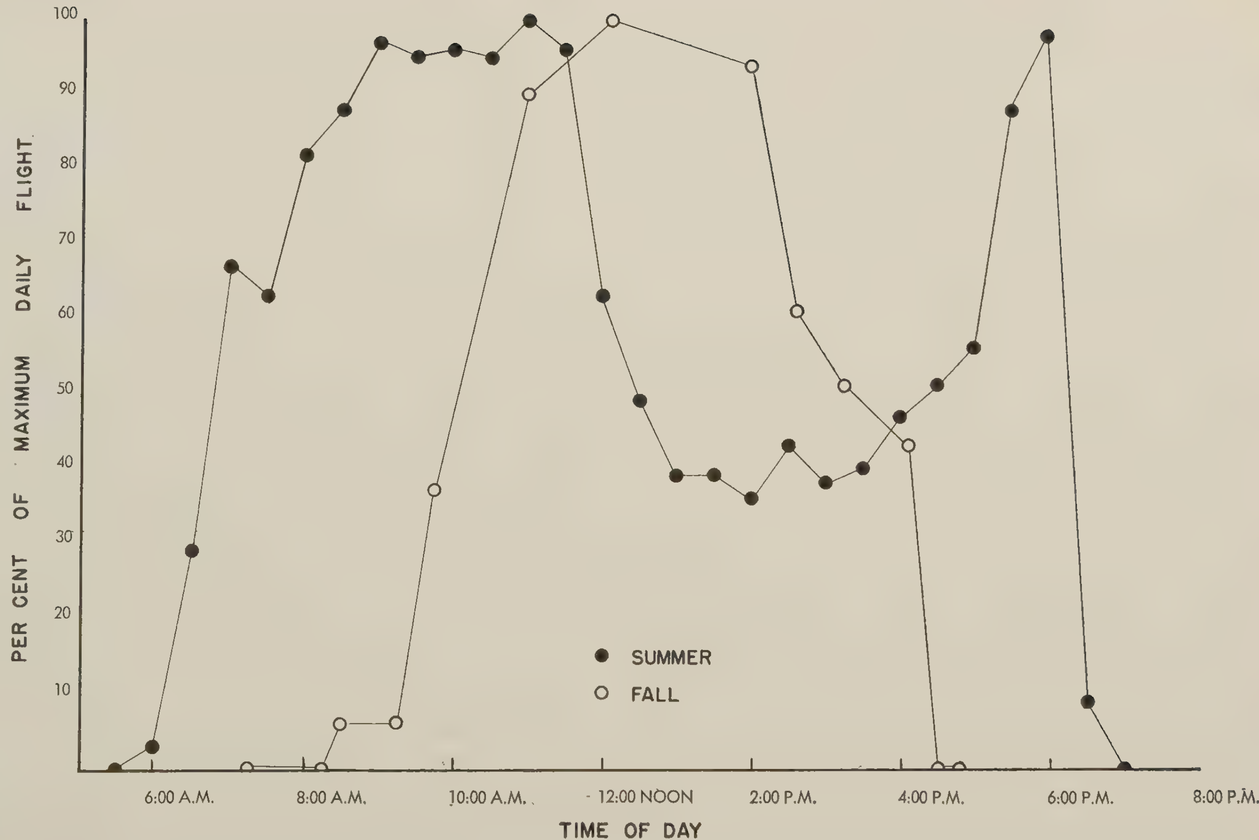

Fig. 21. Intensity of flight activity in relation to time of day during summer (July 28, 1953) and fall (October 23, 1953). (Famoso, Kern County.)

of the air and light may also be limiting in so far as flight is concerned.

Flight activity records were obtained by counts of the butterflies flying across a 30-foot, east-west line and a similar north-south line. All butterflies passing the lines were counted regardless of their direction of travel. The count period was three minutes on each line, or a total of six minutes of flight. Flight activity counts in some cases were made separately for the sexes and for the color phases. In many cases, no separation was made. This procedure appears to be fully justified on the basis that there was no differential diurnal flight pattern of the sexes or the color phases, and no significant difference in body temperatures of the yellow and the white butterflies when they were exposed to the same environmental conditions.

Flight count usually extended from the period of inactivity in the early morning to the time that all flight again stopped, in the afternoon or evening. Occasionally, counts were discontinued because of rain or other factors.

Usually, flights of *Colias* reach a peak of activity in the midmorning and late afternoon, in clear weather during the warmer months of the year, with a decline at midday (fig. 21). On cooler days and during the spring and late fall, there is a single peak which usually occurs at or some time after midday (fig. 21). The spring flight pattern closely parallels that of the fall, but more frequently shows a midafternoon peak. During summer, and from early to mid-fall, when daytime temperatures are high, flight activity declines at midday.

Occasionally, one factor of the physical environment can be singled out as responsible for a particular variation in activity, but usually such variation results from interaction of two or more factors. In general, under field conditions, the greatest single determinant of the insect's ability to fly is body temperature. Unless the temperature reaches a minimum threshold, only forced flight occurs. The same is true if the temperature exceeds a maximum threshold. Although body temperature and the factors which interact to regulate it may be favorable for flight, light intensity may be low and prove limiting.

Initiation of Flight. The upward movement of butterflies on plants, and orientation to the greatest amount of solar radiation are means of attaining a body temperature at which flight can be undertaken and sustained.

The vibration of the thoracic muscles before flight and their activity in flight undoubtedly produce significant amounts of heat which contribute to the body temperature. With large insects, such as the migratory locust (Strelnikov, 1936) and *Samia* (Oosthuizen, 1939), increases in body temperature as great as 10 degrees C have been reported. With *Vanessa atalanta* (Linnaeus), a butterfly approximately the size of *Colias*, Krogh and Zeuthen (1941) found increases of over 4 degrees C due to vibration of the wings and of 7 degrees due to flight in an environment where radiant heat apparently was not an important source of energy.

Colias may frequently be seen flying only short distances, and unusually slowly, during morning coolness, or at any time on cool days. On alighting, the butterflies again orient to receive the greatest solar radiation. If the heat of muscular activity at this time were sufficient to raise the body temperature several degrees, it should have had more significant effects on flight.

TABLE 7

RELATION OF TIME OF DAY, AIR TEMPERATURE, BODY TEMPERATURE, AND LIGHT INTENSITY TO INITIATION OF FLIGHT IN *COLIAS*

Date of observation	Time of day*	Conditions prevailing at time of flight initiation		
		Ambient air temp. at 20 inches	Colias body temp. at 20 inches	Light intensity†
		°C	°C	
April 21	9:00 a.m.	19.0	23.7	.
April 29	9:45 a.m.	20 7	27.0	....
	11:15 a.m.	19.2	23.2	13
	12:15 p.m.	18.2	26.5	....
May 6	8:15 a.m.	22.0	23.5	20
May 15	12:00 noon	15.0	18.0	..
	12:15 p.m.	13.7	16.0	...
May 16	8:19 a.m.	18.2	18.7	17
	8:45 a.m.	18.5	18.5	16
May 17	8:00 a.m.	19.5	21.0	40
July 26	6:00 a.m.	18.0	20.0	30
July 27	6:00 a.m.	20.5	21.7	30
July 28	6:00 a.m.	19.0	21.7	28
September 24	7:45 a.m.	19.5	25.2	9,250
September 25	7:35 a.m.	19.2	22.0	4,750
September 26	7:53 a.m.	18.0	24.7	4,750
September 29	7:25 a.m.	16.2	....	5,700
September 30	7:25 a.m.	15.7	20.0	1,900
October 9	7:15 a.m.	18.5	24.7	5,700
October 10	7:30 a.m.	17.7	24.5	7,600
October 15	8:02 a.m.	16.2	22.2	7,600
October 16	9:35 a.m.	19.0	21 5	5,700
October 17	8:15 a.m.	13.2	20.0	7,600
October 20	8:05 a.m.	11.7	20.2	7,600
October 22	9:05 a.m.	16.0	20.2	7,600
October 23	8:30 a.m.	13.2	17.5	7,600

* On overcast days there may be several periods when flight initiation is observed.
† Light intensity values from April 29 to July 28 are relative values. In September and October the light intensity is expressed in foot-candles.

and these early flights should have been longer. Presumably the explanation is that, in the field environment studied, radiant energy was very important, and the butterflies were warmed sufficiently to initiate flight when they oriented their bodies to the sun, but cooled in flight. In this investigation, flight was not considered to have begun until the butterflies were able to make sustained flight movements, i.e., of more than a few feet. The few individuals that made short, uneven flights of 10 to 20 feet were not considered to indicate the favorable limit of the physical environment for flight.

Initiation of flight is closely correlated with body temperature in the morning, and at other times of day in inclement weather. Flight usually begins at air temperatures between 16° and 19°C and body temperatures between 20° and 25°C. Occasional flights occurred with body temperatures as low as 17.5°C and, on two occasions, flight was delayed until the body temperatures had reached 26.5° and 27°C, respectively. Table 7 summarizes the results of 26 records of flight initiation. These data are further refined in table 8 which presents the range of temperatures at which first flight

TABLE 8
NUMBERS OF FIRST FLIGHTS OF *COLIAS* IN RELATION TO AIR AND BODY TEMPERATURE

Temperature	Number of first flights observed in the field		Number of first flights observed in the laboratory	
	Ambient air temperature	Body temperature	Ambient air temperature	Body temperature
° C				
11.5–12.4	1	0	0	0
12.5–13.4	2	0	0	0
13.5–14.4	1	0	1	0
14.5–15.4	1	0	0	0
15.5–16.4	4	0	1	0
16.5–17.4	0	0	0	2
17.5–18.4	5	2	2	0
18.5–19.4	7	1	0	2
19.5–20.4	2	4	4	3
20.5–21.4	2	2	2	1
21.5–22.4	7	5	2	2
22.5–23.4	0	1	4	5
23.5–24.4	0	4	1	1
24.5–25.4	0	4	1	0
25.5–26.4	0	0	0	0
26.5–27.4	0	2	0	0
Total	26	25	18	16

occurred. Of the 26 occasions observed, flight began on 16 in the 16° to 19°C air temperature range, and on 20 in the 16° to 21°C range. Initial flight occurred at body temperatures between 20° and 25°C on 20 of 25 occasions.

The cause of this variation in the temperature-flight level relationship is not known. Some of the effect may be associated with air movement since, on October 17, 20, 22, and 23, although ambient air temperature was quite low, body temperature approached or fell within the expected range of greatest flight activity. The heat developed by muscular activity may also have contributed to some of the variation observed.

Cessation of Flight in the Evening. Afternoon flight was considered to have stopped when only an occasional butterfly was seen undertaking sustained flight or, in cool weather, when the sustained flights had stopped. This was somewhat difficult to determine since activity usually began to decline 15 to 20 minutes or more before that time. The data collected were not sufficient to assess the influence of body temperature on cessation of flight. It is believed that, if more data had been collected in the early spring and late fall, a greater proportion of the flight cessation could have been accounted for by temperature.

Table 9 summarizes air and body temperature and light intensity conditions when flight stopped in the evening. Usually light was considered to have been the limiting factor to flight when air and body temperatures fell within the range determined by the morning observations as favorable for flight. Flight stopped on 11 of 16 occasions when body temperature was at a level which should have been adequate for flight. On two occasions, light

TABLE 9

RELATION OF TIME OF DAY, AIR TEMPERATURE, BODY TEMPERATURE, AND LIGHT INTENSITY TO CESSATION OF FLIGHT

Date of observation	Time of day	Conditions prevailing at time of flight cessation			Limiting factor†
		Ambient air temp. at 20 inches	Body temp.	Light intensity*	
		°C	°C		
April 29	12:30 p.m.	19.5	21.0	5	light
May 4	5:15 p.m.	25.7	28.5	12	light
May 16	4:45 p.m.	21.7	20.7	15	light
May 17	5:15 p.m.	22.5	25.0	20	light
July 25	5:06 p.m.	16.7	17.5	10	light–temp.
July 27	7:00 p.m.	23.0	21.0	5	light
July 28	7:00 p.m.	22.2	21.5	5	light
September 24	5:00 p.m.	26.0	28.5	2,850	light
September 25	5:10 p.m.	22.7	26.2	2,850	light
September 29	5:20 p.m.	18.7	22.7	1,700	light
September 30	4:20 p.m.	22.7	28.7	5,700	unknown
October 10	5:05 p.m.	21.0	22.0	1,500	light
October 15	4:40 p.m.	18.0	21.5	2,850	light
October 16	4:40 p.m.	18.2	19.2	1,150	light–temp.
October 22	4:20 p.m.	15.0	18.0	3,800	temperature
October 23	4:05 p.m.	20.5	24.0	4,750	unknown

* Light intensity values from April 29 to July 28 are relative values. In September and October the light intensity is expressed in foot-candles.

† Estimate of limiting factor is based on whether the body temperature is adequate for flight activity or lies below the favorable range. For further discussion see text.

and/or temperature may have been limiting, and once temperature seems to have been the limiting factor. Flight ceased on two occasions while light, and air and body temperatures were all within the favorable range for activity.

In considering light intensity in relationship to flight, with the scale used before September 24 (i.e., through August 28), any value below 15 to 20 may be considered limiting to *Colias* flight; after that date, values of less than about 3,000 foot-candles are limiting. During summer months when the evening air temperature remains high, declining light intensity is the major cause of flight cessation.

When either body temperature or light is the factor limiting flight of *Colias*, the butterflies can be induced to fly if neither factor is far below its minimum level. These flights are usually short and, in the case of limiting temperature conditions, slow.

Midday Flight Decline. During summer and from early to mid-fall, when daytime air temperatures are high, the flight of *Colias* undergoes a midday decline. This begins as early as 10:00 a.m. on some days, and lasts until mid- or late afternoon. Its extent and duration are quite variable, and are apparently determined by a combination of several environmental factors. Frequently, the peak activity of the morning is not again attained. In contrast, when the weather is cool, during spring and late fall, a single peak of activity occurs some time after 11:00 a.m. Both activity patterns are illustrated in figure 21.

TABLE 10

PHYSICAL CONDITIONS PREVAILING IN ALFALFA FIELDS AND IN DRY PASTURE DURING MORNING PERIOD OF MAXIMUM FLIGHT ACTIVITY ON DAYS WITH A MIDDAY DECLINE IN ACTIVITY (1953)

Date of observation	Time of day	Type of field	Body temp. at 20 inches	Physical conditions of environment			
				Ambient air temp. at 20 inches	Globe temp. at 20 inches	Atmom. evap.	Wind movement
			°*C*	°*C*	°*C*	*cc/hr.*	
July 25	11:30 a.m.	alfalfa	30.2	42.5	55.2	12.0	slight–medium
July 26	11:30 a.m.	alfalfa	34.2	45.5	61.2	11.1	slight
July 27	10:00 a.m.	alfalfa	38.0	25.2	39.0	15.5	medium
	9:30 a.m.	pasture	37.5	....	46.0	....	medium
July 28	11:00 a.m.	alfalfa	42.0	31.7	48.2	14.3	slight
	9:30 a.m.	pasture	39.0	....	50.0	....	slight
September 25	12:05 p.m.	alfalfa	31.2	25.5	45.7	10.0	gusty
September 29	11:30 a.m.	pasture	32.0	32.5	40.0	13.6	gusty
September 30	9:50 a.m.	alfalfa	28.0	24.7	41.0	7.0	gusty
	11:30 a.m.	alfalfa	30.5	29.7	39.7	16.5	gusty
October 10	9:00 a.m.	alfalfa	25.2	19.2	34.2	5.0	slight–medium
October 20	10:45 a.m.	alfalfa	24.5	19.2	33.0	....	gusty
October 23	11:15 a.m.	pasture	32.7	26.0	38.7	9.5	gusty
Average			29.2	32.7	44.0	11.4	

In an effort to determine the cause of the midday decline, air, body, and globe thermometer temperatures, the evaporative capacity of the air, and the rate of air movement were investigated. Results are summarized in tables 10 and 11 for the morning and afternoon peaks of activity on days with a midday decline, and in table 12, for the days with a single peak. The relationships between body, air and globe thermometer temperatures, evaporative power of the air, and rate of air movement varied greatly.

Body temperature exceeded 38°C only twice at the time of peak activity, and this occurred on the morning of the same day, at separate locations. Maximum afternoon flight activity was not reached in any case before body temperature had dropped below 35°C. On days with only one peak of activity, body temperature did not exceed 33.2°C in any case. In all factors, except rate of evaporation, the maximum reading was lowest on days of a single peak. In the case of evaporation, the lowest maximum reading in the afternoon was below the value on a single-peak day.

The favorable range of temperature and maximum and minimum temperatures which adult *Colias* can endure are not known precisely. Williams and Bishara (1929) reported maximum activity of *Colias edusa* at times when the air temperature was between 34° and 40°C, and no flight was observed when the temperature was over 42°C. As mentioned earlier, the actual temperature which the *Colias* body attains when undisturbed in its normal environment may not be the same as that measured on the thermocouple. The level at which peak flight occurs may be a lower temperature. The body temperatures of individuals that can seek shade and moisture are certainly maintained at considerably lower levels than those of individuals

Table 11

PHYSICAL CONDITIONS PREVAILING IN ALFALFA FIELDS AND IN DRY PASTURE DURING AFTERNOON PERIOD OF MAXIMUM FLIGHT ACTIVITY ON DAYS WITH A MIDDAY DECLINE IN ACTIVITY (1953)

Date of observation	Time of day	Type of field	Body temp. at 20 inches	Physical conditions of environment			
				Ambient air temp. at 20 inches	Globe temp. at 20 inches	Atmom. evap.	Wind movement
			°C	°C	°C	cc/hr.	
July 25	5:00 p.m.	alfalfa	30.5	26.2	38.5	9.8	slight
July 26	3:30 p.m.	alfalfa	35.0	41.7	53.7	13.8	slight
July 27	6:00 p.m.	alfalfa	27.7	28.2	35.7	11.0	gusty
	7:00 p.m.	pasture	28.0	....	30.5	....	gusty
July 28	6:00 p.m.	alfalfa	27.0	26.2	34.2	12.0	gusty
	6:00 p.m.	pasture	30.5	....	40.0	....	gusty
September 25	2:50 p.m.	alfalfa	34.5	28.2	43.7	10.8	gusty
September 29	3:35 p.m.	pasture	31.5	31.2	42.2	12.9	gusty
September 30	3:25 p.m.	alfalfa	31.2	24.7	38.0	8.0	very slight
	4:00 p.m.	pasture	30.7	30.7	37.7	12.7	gusty
October 10	2:05 p.m.	alfalfa	30.0	24.5	41.0	10.0	medium gusts
October 20	3:40 p.m.	alfalfa	29.0	24.7	34.2	....	gusty
October 30	2:50 p.m.	pasture	29.2	27.5	35.2	12.0	gusty
Average			30.3	28.5	35.7	11.4	

that must remain oriented and exposed to direct solar radiation on thermocouples.

The main source of heat and therefore of body temperature, during the daylight hours, is direct solar radiation. However, the extreme to which body temperature will increase is modified by ambient air temperature, air movement, and evaporative cooling. If the body temperature approaches the maximum favorable limit (estimated here as 38°C), the butterflies will attempt to modify their body temperature to some extent through orientation to the incoming radiation, by seeking shelter in the shade of plants or coming to rest on a damp surface, such as pond scum or wet soil. This lowers body temperature and also reduces the heat created by flight.

Air temperatures in excess of 35°C appear to create an additional cooling problem for the insect. The data indicate that *Colias* can maintain a temperature lower than that of the air, when the latter becomes too great. Evidence for such a mechanism was indicated by periods in which air temperature exceeded body temperature by several degrees. These occurred on three occasions in midsummer. This mechanism is apparently determined by the insect's water relationships and water loss since individuals deprived of a water source do not survive very long under hot, dry conditions. Although body temperatures in some instances ranged as much as 11 degrees C below air temperature, the insects were not able to maintain a lower body temperature long (some went as high as 42°C before death) when placed on thermocouples and oriented perpendicular to the sun. The actual temperature attained by the *Colias* and the need for cooling may not be so great as indicated here. Under "normal" conditions, the butterfly would be

TABLE 12

PHYSICAL CONDITIONS PREVAILING IN ALFALFA FIELDS AT THE TIME OF PEAK FLIGHT ACTIVITY ON DAYS WITHOUT A MIDDAY DECLINE IN ACTIVITY (1953)

Date of observation	Time of day	Body temp. at 20 inches	Physical conditions of environment			
			Ambient air temp. at 20 inches	Globe temp. at 20 inches	Atmom. evap.	Wind movement
		°C	°C	°C	cc/hr.	
April 21	12:00 noon	33.2	27.0	45.2	9.2	medium
June 14	11:30 a.m.	....	29.5	40.7	14.3	med. to fast
September 24	11:45 a.m.	30.7	27.7	41.0	10.2	slight
September 29	3:05 p.m.	33.0	26.5	42.7	8.7	gusty
October 15	1:20 p.m.	27.0	21.0	32.0	10.2	med.-strong
October 16	2:45 p.m.	23.5	23.0	30.2	7.8	gusty
October 22	1:30 p.m.	26.2	21.7	34.0	....	gusty
October 23	12:05 p.m.	30.2	21.2	36.7	9.5	gusty
Average		29.1	24.7	37.8	10.0	

orienting parallel to the sun's rays, seeking shade, and or resting on a damp surface where the heat loss from water evaporation provides cooler conditions.

The evaporation rate of free water may indicate the rate of "desiccation" of *Colias*. This desiccation may be of great value in maintaining body temperature below a critical high level through heat uptake in evaporation. If, however, the loss becomes great and the butterflies do not have recourse to an adequate supply of water or nectar, flight must be curtailed. Under severe conditions of desiccation, a sharp reponse in activity of the butterflies may occur if the evaporative power of the air is decreased to any appreciable extent. Such an occurrence is not uncommon and is well illustrated in figure 22. In this case a decline in the rate of evaporation of water from a Livingston atmometer of 17.5 cc per hour to 10.8 cc per hour was correlated with an increase in flight count of from 201 to 305. The rate of evaporation then increased by 1.2 cc per hour and the flight count declined by 45. In a similar instance on July 28 (the following day), a decrease in the evaporation rate of 4.8 cc per hour was correlated with an increase in activity of *Colias* from 206 to 251. Following this, the rate of evaporation again increased 3.8 cc per hour, to 14.6, and activity decreased by 28, to 223.

The factor responsible for the change in rate of evaporation on both days was a mass of cooler, more humid air which moved through the area. In addition to a decrease in the rate of evaporation, the air and body temperatures showed a drop of 2.2 degrees, while the globe thermometer showed only a very minor change in temperature. These declines in temperature were not sufficient alone to stimulate flight. Body temperature had previously dropped to 35°C which was already within the range of activity. These changes occurred at 3:30 p.m. on July 27, 1953, and at 2:30 p.m. on July 28, 1953, both near the usual time for temperature and evaporation to start declining.

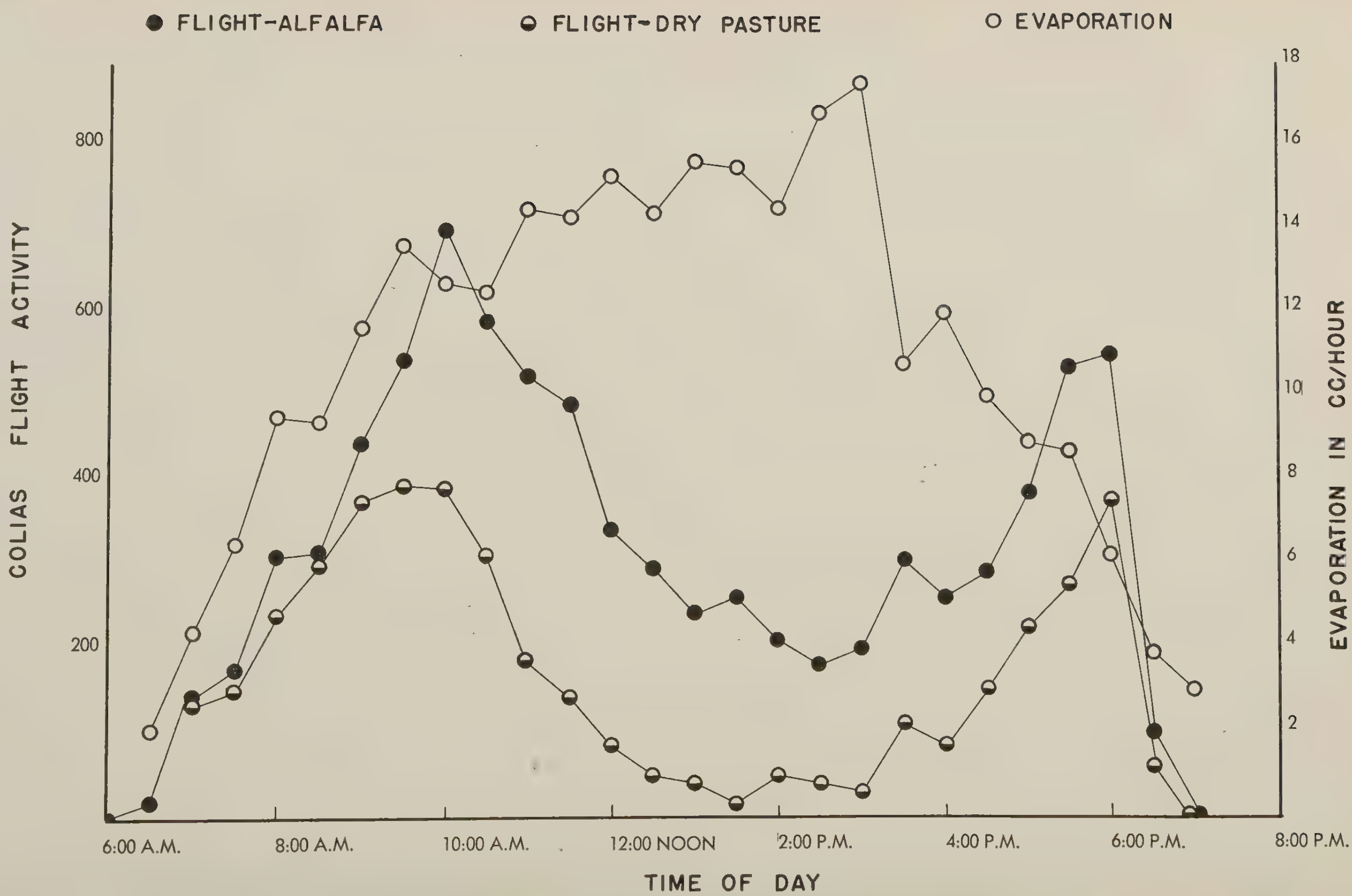

Fig. 22. Intensity of flight activity of *Colias* in alfala and in dry pasture, in relation to evxaporation of water from a Livingston atmometer in the alfalfa field. (Famoso, Kern County, July 27, 1953.)

Air movement is responsible for considerable variation in the rate of evaporation and desiccation. In the case of *Colias* in flight, this factor alone is less significant, but with respect to the humidity of the air over an alfalfa field or in the general area, it may have a large influence, since the moisture given up by the alfalfa plants and the soil is quickly replaced by dry air from near-by unirrigated areas. Wind largely influences air and body temperature, and evaporation, and is of only minor direct significance with respect to flight at the velocities normally encountered.

Laboratory Experiments

To examine the relationship between flight activity, body temperature and light intensity further, a series of experiments were conducted in an environment cabinet in which either light or temperature could be modified. This cabinet has been described by Stern (1952). During all temperature tests, light intensity was maintained at or above 500 foot-candles. In 13 of 16 trials, flight commenced and/or ended as the body temperature exceeded or dropped below a 19° to 23° C range. In the three remaining cases, flight began as the body temperature reached 17° and 24° C, respectively.

In the laboratory, flight began at or slightly below the minimum range of temperature at which flight was possible in the field. The results of 25 field and 16 laboratory tests are shown in table 8 (p. 609), indicating the number of times flight began at each degree increment, with no flight occurring below that level. The reason for this differential is not known. The light qualities and ambient air temperature in the laboratory and field are not the same. In the laboratory, however, the light intensity was more constant. Light was provided by a bank of 13 daylight-type fluorescent tubes, as described by Stern (1952). Air temperature was higher in relation to flight in the laboratory, presumably as a result of lower radiation intensity.

In laboratory experiments on light intensity, the temperature was held at 23° C ± 1.5°. Light was regulated by turning off or on one or more of the 13 fluorescent tubes. The intensity in each case was measured with the same exposure meter that was used on and after September 24 in the field experiments. Flight occurred readily at all times when the light intensity exceeded 300 foot-candles. Between 210 and 300 foot-candles some sporadic flight was made, by one or two of the four to six experimental butterflies used. Below 210 foot-candles no flight was attempted although the butterflies would crawl about to a limited extent at intensities as low as 100 foot-candles.

No explanation is available to account for the difference in light intensity at which flight is initiated in the field and under laboratory conditions. The differences between field and laboratory with respect to light quality, importance of long-wave radiation, and preconditioning of the insects may offer possible hypotheses.

Rate of Flight

A series of counts were made on September 23 to determine if the rate of flight of *Colias* was affected by temperature. The time, in seconds, required

for a butterfly to fly a distance of 20 feet was recorded at intervals through the day from the time sustained flight started in the morning until it stopped in the evening. The results were as follows:

TIME OF DAY	RATE OF FLIGHT *ft/min.*	AIR TEMPERATURE °C
8:00 a.m.	270	19.0
8:25 a.m.	276	21.3
8:55 a.m.	318	24.5
9:30 a.m.	288	26.5
10:14 a.m.	306	28.0
10:50 a.m.	276	27.5
11:40 a.m.	330	26.0
12:24 p.m.	384	28.0
2:00 p.m.	300	25.0
2:40 p.m.	366	23.0
3:25 p.m.	324	25.5
4:05 p.m.	378	27.0
4:30 p.m.	330	25.5

Flight in the early morning and after sustained flight has stopped in the afternoon is usually so erratic that it cannot be measured by the above method. During this time of day the flight is distinctly slower than at any other time, and is of short duration. During the remainder of the day the rate of flight is nearly constant.

DISCUSSION AND CONCLUSIONS

Solar radiation at the earth's surface, unless interrupted by clouds, dust, or smoke, will describe a curve of symmetrical increase and decrease. Directly associated with this curve is that of light intensity. However, light reaches its near-maximum intensity at an earlier hour of the day, and remains steady through the midday period. As solar radiation warms the earth and atmosphere, relative humidity declines and rate of evaporation from atmometers increases. These three changes are directly associated with the increase in air temperature although rate of evaporation is also influenced by vapor pressure. The unequal warming of the atmosphere creates air currents which in turn also modify the rate of evaporation. With the rapid decline of solar radiation in the afternoon, light intensity, air temperature, and rate of evaporation begin to decline, and relative humidity begins to increase. Wind relationships are more variable and may exert considerable influence on air temperature and evaporation as a result of mass air movements.

The relationship between the many factors of the physical environment and the flight responses of *Colias philodice eurytheme* is extremely complex. The observed actions of *Colias* under certain extremes of physical conditions were responsible in some degree not only for the selection of the physical factors investigated, but also for the choice of responses that were studied. Figure 23 shows a diagram of some of the more significant relationships. The necessary simplification is so great that much of the inde-

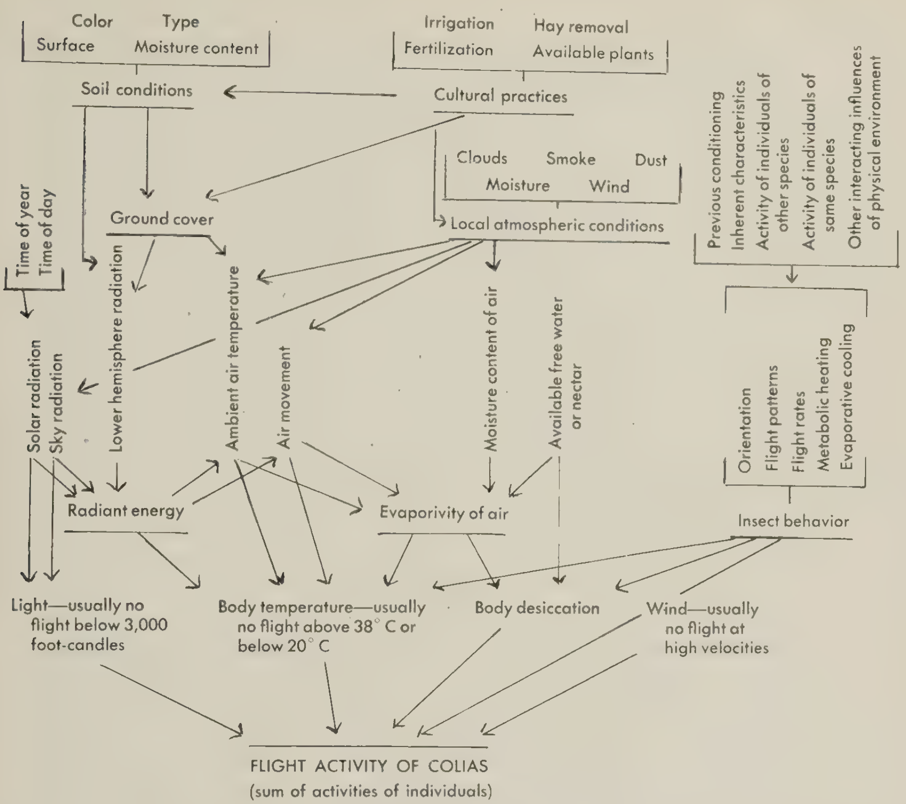

Fig. 23. Diagram shows some of the more significant relationships between physical environment and flight response of *Colias*.

pendent importance of individual factors is masked; however, the diagram will be of assistance in the following discussion.

The interaction of physical factors that determine body temperature is significant because none of those factors acts alone. Solar radiation appears to be the most important agent, but its effect is in turn modified by air temperature and the cooling of the insect through evaporation. When radiation intensity is sufficiently high and air temperature is not too low, *Colias* increases its body temperature by orienting perpendicular to the sun. When the relationship between radiation and air temperature is near the level at which *Colias* are capable of flight, they collect on bare soil and highway pavement, which are warm and which help to increase body temperature. Flight activity also contributes, to a minor extent, to body temperature (Oosthuizen, 1939).

When the body temperature is nearing the critical high level, the *Colias* appears able to regulate it in several ways. Flight activity decreases, and may cease in some areas, thereby reducing the heat from muscular activity. When they stop flying, the butterflies come to rest in plant shade, where they orient parallel to the sun's rays, or on moist soil or algal scum, where

evaporation of water cools the air and the insect body. *Colias* may also take water while at rest, which permits the body to cool by evaporation without desiccation. This last factor is of great significance in survival in the hot Central Valley of California.

Under near extreme levels of other factors, however, desiccation can limit flight, even if the body temperature is below the upper critical level. This is most evident where *Colias* has no source of water or nectar. On the other hand, at its period of peak intensity, solar radiation may not limit flight, because the combined effect of low air temperature and, perhaps, evaporation brings the body temperature within the favorable range for activity. These conditions frequently prevail during the spring and fall.

Light intensity is the only factor considered that will, alone, cause cessation of flight when all other factors are favorable. Sometimes one or several of the other factors will stop flight before light intensity has declined to a point where flight must stop. During midsummer, on some hot days, body temperature was adequate for flight until well after sunset, but flight still declined and stopped when light dropped below 3,000 foot-candles. During the entire year, light is always adequate for flight in the morning before the insects have warmed to the temperature at which flight can start.

The relationship of color of the females to season and to time of day needs more intensive investigation. The present research found no distinct variation in the activity ratio of white and yellow females throughout the day. This is in opposition to the findings of Hovanitz (1948), and further work on the problem is necessary. Nonselective sweep counts, coupled with detailed observation of normal flight activity in areas of dense population, must be made in seeking a satisfactory solution to this problem.

Body temperature measurements are not completely satisfactory as made with the present probe thermocouples which disrupt the insect's physiology. Further investigation of smaller elements may be of assistance, but the solution may lie in the development of artificial butterflies. Determination of the radiation absorption characteristics of the yellow and the white females and of the male may help us to understand why there are no differences in body temperature among these forms. Better correlation of the relationship between body temperature and the globe thermometer-air combination is needed in order to explain some of the reasons for extreme variation between the two. Air movement appears to be one of the critical factors in this situation. Information on air movement is also needed for a better interpretation of atmometric evaporation rates. The information so provided would help in interpretation of problems of desiccation and of body cooling.

Instruments used at 60 inches are representative of the macroenvironment, and data derived from them compare well with standard weather shelter data in the immediate area. The relationship between the factors at 20 and at 60 inches is the same, but the degree of influence of one factor on another may be greater at the lower height. While the variation in factors from one location to another in the same local area is usually minor at 60 inches, it may be very large at a height of 20 inches. At 20 inches, instruments are at the upper limit of the zone of steep gradient-change

for some factors. They are, however, in the region in which adult *Colias* spend a great portion of their time when not at rest.

The effect of prior conditioning to one or several factors of the environment on responses of the butterflies to these or other factors has been given very little attention. An indication of conditioning to light was evident in the laboratory investigation, but was inconclusive. Since conditioning may be a factor in any of the responses, this phase is in need of study.

Most of the unsolved problems concerning the relationship of *Colias* to its physical environment require the development of more refined instruments. Some of those used in this investigation need greater refinement, although they have been used successfully in a number of other types of agricultural investigations.

With the continued efforts of workers from fields associated with micrometeorology and the development of instruments, such as the Agricultural Engineering group at the University of California, the necessary tools will be developed. Application of this equipment to problems in ecology will then lead to a better understanding of the relationship of the physical environment to insect activity.

SUMMARY

Observations of *Colias philodice eurytheme* in the field indicated a need for investigation of the physical environment if the insect's activities were to be understood. The factors of the physical environment are numerous and complex. Within the limitations of manpower and available instruments, factors selected for study included solar and other radiation, light, air temperature, and moisture relationships. Body temperature and flight activity were selected as factors of response to the physical environment. Since populations of *Colias* include males and both white and yellow females, the population relationship of these categories and their individual response to the physical environment were investigated. Some of the response factors were further studied under controlled laboratory conditions.

Solar and sky radiation was measured as a unit with a "total hemispherical radiometer." Its intensity was found to transcribe a symmetrical curve which peaks at solar zenith unless interrupted by clouds or other obstructions. During clear weather the sky radiation remains at near 100 B.T.U./sq. ft./hr. at night, and increases to about 460 B.T.U. sq. ft./hr. at midday. Clouds, dust, or smoke may strongly influence the peak intensity which can be reached by solar radiation.

Mean effectual radiation was investigated with globe thermometers. These instruments indicated temperatures as much as 1 to $1\frac{1}{2}$ degrees C below air temperature at night, and 9 degrees above air temperature during midmorning at a height of 60 inches. A globe thermometer at a height of 20 inches will usually remain 3 to 5 degrees lower at night and 1 to 2 degrees higher during the daylight hours than will a globe thermometer at a height of 60 inches. These instruments are strongly affected by wind or any factor which interrupts solar radiation, and by varying types of groundcover.

Light intensity, measured with photographic exposure meters, was found

to increase steadily, in clear weather, and reach near maximum in early to midmorning, with a comparable decline in the late afternoon. Light intensity reaches about 10,000 foot-candles on a clear day, with much variation due to clouds, smoke, and dust. Reductions as a result of these factors may be as great as 6,000 foot-candles or more.

Ambient air temperature at 20-inch heights is usually lower at night, higher during the day, and undergoes much more fluctuation than at 60 inches. It is also strongly regulated by the type of groundcover.

Water relationships consisted of measurement of the relative humidity and rate of evaporation at 20- and 60-inch heights. Relative humidity usually reaches 80 to 95 per cent in the predawn hours, and drops to about 20 per cent at midday. It may be from 2 to 10 per cent higher at the lower height. Evaporation from a Livingston atmometer is strongly regulated by humidity factors, air movement and, when comparing the 20- and 60-inch heights, by the type of groundcover. In an alfalfa field, the rate of evaporation at 20 inches is usually from 2 to 6 cc per hour less than at 60 inches.

Large fluctuations in the population and in the ratio of male to female *Colias* occur from field to field. The ratio of white to yellow female *Colias* is near 1:1 in the Wasco area of Kern County during the summer months. The body temperatures of the sexes and color phases of *Colias* were not found to be greatly different, and are considered to be equal under similar physical conditions.

Body temperature of *Colias* is largely regulated by solar radiation intensity, which may be modified by clouds and other physical factors. In the absence of direct solar radiation, it will equal air temperature. Radiation from the ground and other objects is of negligible value, alone, as a source for body heat. The effectiveness of solar radiation as a source of body heat is regulated by *Colias* through its orientation to the sun. Orientation is perpendicular to the path of the sun's heat when air and body temperatures become very high. *Colias* will also seek cool locations at which to rest.

Flight activity is one of the most indicative responses of *Colias* to its physical environment. Initiation of flight in the morning is usually regulated by body temperature, which will be between 20° and 25°C. During cool weather, cessation of flight in the evening may be the result of a decrease in body temperature. During hot weather, it is frequently the result of declining light intensity. Light intensities of less than 3,000 foot-candles are considered limiting. Laboratory investigations of light intensity and body temperature in relation to initiation and cessation of flight substantiate these results. A midday decline in flight activity will frequently occur during hot weather, when butterflies seek shelter and water. This response is evident when solar radiation intensity and air temperature are high enough to increase to a critical level. This also occurs when there is a high rate of water evaporation, which may indicate desiccation. Although flight activity of *Colias* is strongly regulated by the preceding factors, the rate of flight has not been found to increase with an increase in temperature except near the minimum level at which flight can occur.

ACKNOWLEDGMENTS

The authors wish to express their sincere appreciation to the several staff members of the University of California and friends who were helpful throughout the various phases of research reported in this paper. In particular, they wish to acknowledge Roderick Craig, C. F. Kelly, J. W. MacSwain, Frank Pitelka, and Richard Doutt for their interest in the project, advice, and helpful suggestions in the preparation of the manuscript. They wish also to thank Lloyd Andres, William W. Allen, Douglas E. Bryan, and Vernon M. Stern who were helpful in the field and laboratory. Finally, they wish to acknowledge the great assistance of the Kern County Land Company and El Solyo Farms for permitting free access to their facilities.

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